



TICKS AND THEIR SMALL MAMMAL HOSTS

A STUDY ON DYNAMICS AND HOST
RELATIONS OF IXODES RICINUS
AND I. TRIANGULICEPS (ACARI)

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1. I AM SURE THAT A MAN
WHO IS A MAN
FROM THE
COUNTRY
CITY
CITY



The thesis is mainly a summary of the following papers:

I. Distribution, host relations, and seasonal occurrence of
Tachinid flies (Diptera: Tachinidae) on reindeer
Nilsson, A., 1974, 233-241.

II. Host relations of Tachinid flies (Diptera: Tachinidae) on reindeer
Nilsson, A., 1974, 241-247.

III. Seasonal occurrence of Tachinid flies (Diptera: Tachinidae) on reindeer
Nilsson, A., 1974, 247-253.

IV. Parasitism of Tachinid flies (Diptera: Tachinidae) on reindeer
Nilsson, A., 1974, 253-259.

V. Spatial distribution of Tachinid flies (Diptera: Tachinidae) on reindeer
Nilsson, A., 1974, 259-265.

VI. Host relations of Tachinid flies (Diptera: Tachinidae) on reindeer
Nilsson, A., 1974, 265-271.

They will be referred to by their titles in the
following:

Once upon a time there was a little female
tick sitting in a tree high over the green
pasture with grazing cattle. She waited
and waited. All of a sudden she felt that
wonderful smell of sweat, she loosened her
grip and, landing on something hairy she
crawled to the barest and warmest spot,
pushed out her proboscis, and started to
suck. When she was several times her
original size she fell to the ground and
her life cycle came to an end.

But she was not going to have any
young because it was not a cow she had
landed upon. It was the apparatus of a
nasty ecologist who had walked under the
tree with a plastic sheet with butyric
acid and cattle hairs which covered a
plastic tube filled with body-temperature
water.

(Bengt-Owe Jansson 1971)

The thesis is mainly a summary of the following papers:

- I. Distribution, host relations, and seasonal occurrence of *Ixodes trianguliceps* Birula (Acari) in Fennoscandia. Nilsson, A. 1974. - Folia parasitol. (Praha) 21: 233-241.
- II. Host relations and population changes of *Ixodes trianguliceps* (Acari) in northern Scandinavia. Nilsson, A. 1974. - Oikos 25: 315-320.
- III. Seasonal occurrence of *Ixodes ricinus* (Acari) in southern Sweden. Nilsson, A. 1978. Submitted to Holarctic Ecology.
- IV. Parasitism of female *Ixodes trianguliceps* by the males. Nilsson, A. 1975. - Oikos 26: 295-298.
- V. Spatial differentiation of ectoparasites on small mammals. Nilsson, A. 1978. Submitted to Holarctic Ecology.
- VI. Host selection and movements of *Ixodes ricinus* larvae on small mammals. Nilsson, A. and Lundqvist, L. 1978. Submitted to Oikos.

They will be referred to by their Roman numerals in the following.

Ticks and their hosts in Scandinavia

Two of the three tick families are represented in Scandinavia, viz. Argasidae and Ixodidae. Argasids are found mostly in warm and xeric areas and live and breed primarily in the nests and burrows of their hosts. They are tough and leathery and feed rapidly. Therefore they do not have to leave the habitation of the host. Two species have been recorded from Scandinavia: Argas reflexus (Fabr.) in pigeon houses (Arthur 1955) and A. vespertilionis Latr. on bats. The hard ticks (Ixodidae) have a dorsal scutum. They engorge slowly and must stay on their hosts for several days; the sucking time is dependent on tick and host species and developmental stage of the tick.

Some ixodids are confined to birds. Ixodes lividus (Koch) is restricted to the sand martin (vide Ulmanen et al. 1977), I. uriae White to colony-living seabirds (Tambs-Lyche 1943), and I. arboricola Schulze et Schlottke to hole-nesters (Haarløv 1962, Brinck et al. 1965, Saikku et al. 1971).

Other ixodids are bound to mammal hosts, viz. I. hexagonus Leach on e.g. hedgehog, mustelids, the badger, and the red fox and I. trianguliceps Birula on burrowing small mammals (I and II). I. ricinus L. and Haemaphysalis punctata Can. et Fanz. may infest a variety of birds and mammals but also lizards.

A number of other ixodids have been recorded occasionally, e.g. I. caledonicus Nuttall from starling (vide Mehl 1970), I. unicavatus Neum. from cormorant (Schulze 1930), I. canisuga Johnston from a nest of the hedgehog and I. arvicolae Warburton from a nest of "mouse" and rat (Arthur 1955).

A species which seems to have settled recently in Scandinavia is the Kennel tick, Rhipicephalus sanguineus (Latr.), which has been brought by imported dogs in to Sweden (Christenson pers. comm.) and Denmark (vide Haarløv 1973) and seems to thrive even in town apartments.

Species of Hyalomma are more or less regularly found on migrating birds in spring (Arthur 1952, Brinck et al. 1965, Saikku et al. 1971). Hyalomma spp., Amblyomma spp. are found on imported snakes, lizards, and tortoises.

Most species have been recovered in the southern parts of Scandinavia only, but I. uriae, I. lividus and I. trianguliceps also in the north.

Small mammals are in Scandinavia infested by I. ricinus and I. trianguliceps, and in restricted areas also by H. punctata. This thesis is a study on the dynamics of the two Ixodes species and the relations to their small mammal hosts.

Life history

Being an important vector for several pathogens, I. ricinus has been extensively studied (vide Arthur 1962 and Balashov 1968). The information on the ecology of I. trianguliceps is scarce. Randolph (1975a), however, presented a model of its life cycle.

I. ricinus and I. trianguliceps are 3-host ticks, i.e. they use 3 different host specimens to complete their developmental cycle. As mentioned above, I. ricinus is able to infest a great variety of species. However, different developmental stages are more or less confined to different groups of hosts. Thus, the larger developmental stages, nymphs and adults prefer larger host species, while the larvae frequently infest smaller hosts, as small mammals.

When off the host, I. ricinus lives in the field layer of the vegetation (to some extent also among bushes). After hatching of the eggs, the larvae stay inactive for some time (often several weeks). During this period they are highly clumped and there is no tendency for dispersal. After some time the ticks move upwards in the vegetation and adopt a waiting position and are then prepared to climb passing animals. During this period and when on the hosts the ticks are regarded as active. In the waiting position the tick is exposed to wind and sun and thus to water loss by evaporation. The tick therefore now and then moves down to a level of higher relative humidity near the ground and there compensates the water loss. The time spent in the waiting position is short. It has been estimated for adult females to be on average 9 days altogether (Lees and Milne 1951).

When active, the I. ricinus larvae still have a strong tendency to keep together (Arthur 1962) which may decrease the evaporation from the body and allow them to stay active for a longer time and so increase the chances of encountering a host. After feeding and moulting, nymphs and adults behave in about the same way as the larvae, although there are less or no gathering tendencies.

The seasonal occurrence of active ticks in the vegetation and thus on the hosts is a result of the life cycle of the ticks. In I. ricinus the light regime induces a diapause in winter (vide Balashov 1968). Increasing temperature seems to play an important role for the onset of activity in spring. There is in South Sweden a rapid increase in activity which culminates in May - June for larvae at inland localities and about one month earlier at the coast. The activity of the nymphs starts earlier than that of the larvae. In autumn, however, the peaks for larvae as well as for nymphs occur in September. Adult I. ricinus showed a somewhat different activity pattern with three peaks in spring, in summer and in autumn. Very few I. ricinus are found to be active in winter (III).

I. trianguliceps larvae are to some extent active also in winter, but similarly to I. ricinus there are two activity peaks. The first occurs in April and the second in September (I). Diapause induced by the light regime is supposed not to occur in I. trianguliceps (Randolph 1975 a).

Host finding and attachment (VI)

According to Lees (1948) host finding and attachment is ensured by three behavioural reactions, viz. 1) orientation responses leading to favourable waiting postures in the vegetation, 2) a direct response to an approaching animal by taking up the "questing posture" and 3) reactions associated with climbing the host and choosing attachment sites.

The behaviour of I. trianguliceps within the burrows of the hosts is unknown. For I. ricinus, however, the behavioural

pattern may be described as follows, by referring to the above mentioned 3 reactions:

1) The distribution of the ticks in the vegetation varies vertically between developmental stages. Adult and nymphs usually climb higher up in the vegetation than the larvae and are in different ways exposed to different host categories. The distribution is horizontally clumped, especially in the larvae. Due to dispersal by hosts, there is a randomization in the horizontal distribution of nymphs and larvae.

2) In the vegetation the ticks sit with their forelegs folded. When a host is approaching, the legs are stretched forwards ("questing posture").

3) The questing posture is induced by different stimuli: sudden vibration of plants, sudden darkness, but also by host odour and warmth. The first two are supposed to play a major role for I. ricinus when hosts pass the tick. The reaction seems to be rather unspecific; ticks attach to most objects they encounter. This is easily observed when dragging a blanket over the grass or when approaching e.g. a forceps to the ticks. A prolongation of the last two stimuli may at small distances induce active crawling towards the host.

After the ticks have climbed the host, they move actively on the host body. The movements are mostly directed against the direction of the fur hairs and result in a concentration of ticks at the head of the host (VI). These movements differ in direction and speed depending on host species. I. ricinus move larvae faster on Apodemus sylvaticus L. than on Clethrionomys glareolus Schreb., while the ticks move hardly at all on Sorex araneus L. There is also a difference between host species regarding the orientation of the ticks on the host body. Immediately after the ticks has been placed on the body, most specimens hide in the fur for a short time. They then become visible and move towards the head; all movements occur on the fur surface. The movements are more determined on A. sylvaticus than on C. glareolus. Thus, after a short time there is an aggregation of ticks on the head of A. sylvaticus. On C. glareolus the major part of the ticks move towards the head, but

several move in other directions, resulting in a less concentrated distribution on the host body. Probably disorientated ticks drop without attaching to the host.

The nymphs of I. ricinus also move towards the head of the rodent hosts. After a few minutes, however, the majority leaves the host. Adult ticks do not respond to the rodent fur by a directed movement and stay on the host usually less than one minute.

Predilection places (V)

I. ricinus larvae as well as I. trianguliceps attach mainly on the head of the host. I. trianguliceps larvae are almost exclusively confined to the ears, while other developmental stages may occur on other parts of the head and occasionally away from the head (Randolph 1975 b). Larvae of I. ricinus prefer the ears of rodents, but to a lesser degree than the larvae of I. trianguliceps. I. ricinus larvae may occur on other short haired or bare parts of the host body, but mostly it is found on the head. Thus, the numbers of larvae on the head of A. flavicollis Melch., A. sylvaticus and C. glareolus were 78.6 %, 88.0 % and 89.9 %, respectively, of the total numbers of attached ticks. On S. araneus 65.5 % of the I. ricinus larvae were found on the head, while 20.2 % and 10.1 % were found on the anterior and posterior part of the back, respectively. This is explained by the behaviour of the tick larvae on the host body. The movements of the larvae on S. araneus are restricted; the larvae probably stay at about the same site, to which they are introduced. This means a more widespread distribution on the S. araneus body, than on the other host species.

The distribution on the host body may be affected by various factors.

1) A mechanical interference of the host. It seems likely that the evolutionary response to such an interference has resulted in a division of body areas of the host between species

or groups of parasitic species. Thus, attached (immobile) species like ticks and chiggers are primarily found on the head, where they are out of reach of direct predation by the host. Most likely this distribution is not a result of the elimination from other parts of the host body. As was found for I. ricinus larvae, there is a directed and determined movement towards their predilection places. Species which inhabit areas where the host can reach them are all small and/or very mobile, viz. fleas, lice and gamasid mites.

2) On body areas where species meet, there might be a segregation in time or in space. In the tick species which inhabit both the ears and the rest of the head, no differentiation as regards predilection places could be demonstrated, mostly probably due to a constant low abundance of I. trianguliceps. The occurrence differed slightly, however, during different seasons (I and III). Among fleas, lice and gamasid mites there is a marked differentiation in choice of body areas. Such differentiation may be evolutionary fixed or simply be a result of interference when the species meet.

3) Abundance. At low abundances of I. ricinus larvae, the ears of rodents are strongly preferred. With increasing abundance, the relative infestation on the ears decrease, while it increase on the rest of the head. S. araneus differs, however: with increasing density the head infestation decrease relatively, while the number of ticks on the ears and the back increase. The same enlargement of the habitat with increasing abundance is observed for Laelaps agilis (Koch) on A. flavicollis.

Feeding

The transition of free-living ticks to a parasitic life is connected with profound morphological and physiological changes in their bodies (Balashov 1968), but also in their behaviour. Owing to these changes the feeding tick may be regarded as a particular developmental stage or phase.

The time the different developmental stages of I. ricinus

feed may be summarized as follows: larvae 2 - 6 days, nymphs 2 - 7 days and adult females 7 - 11 days (own data and Balashov 1968). For I. trianguliceps feeding time seems in general to be somewhat longer (Randolph 1975a). The feeding time is dependent on the host species (Balashov 1968). There was no such difference, however, for I. ricinus larvae on rodents.

The weight of the engorged I. ricinus larvae differs, however, between the host species. On A. sylvaticus the average weight was 0.497 mg and on C. glareolus 0.459 mg, the difference being statistically significant ($0.05 > P > 0.01$) (VI).

The feeding of males differs markedly from that of females, nymphs and larvae. I. ricinus males do not feed on experimental rabbits or guineapigs and are able to mate and fertilize without a blood meal. In I. trianguliceps, however, as in some other species living on small mammals with well-defined nests (Moorhouse and Heath 1975) the males regularly feed on partially or fully engorged females of the same species (IV). The males leave distinct scars on the engorged female. 45 of 162 examined females of I. trianguliceps had been attacked by males in this way. The number of scars increased with increasing degree of engorgement of the female. On at least partially engorged females the scar frequency was 41 %. The scars occurred mostly near the genital opening, which suggests that the males feed in connection with copulation. The high scar frequency also suggests that mating in I. trianguliceps normally occurs on the small mammal host.

Host relations

Although the two species I. ricinus and I. trianguliceps overlap in their choice of hosts, there are differences in their choice of hosts relating to the developmental stage of the tick species. In I. ricinus the larger stages (nymphs and adults) are seldom found on small mammals, which, however, are important hosts for the larvae. Also between the small mammal species, there are sometimes great differences in the occur-

ce: of the larvae. In habitats favourable to I. ricinus in southern Sweden, Apodemus spp. C. glareolus and S. araneus are the most common small mammals. A. sylvaticus is the most infested species followed by C. glareolus and S. araneus. Also within the host species there is a considerable variation in infestation which could be referred to the different functional categories of the host (VI).

I. trianguliceps occurs throughout Fennoscandia except for the northernmost parts and the high mountain areas of Norway and Sweden (I). In the southern parts the species is confined to about the same hosts as I. ricinus larvae but prefers S. minutus L. and C. glareolus before species of Apodemus and S. araneus. In the north, Apodemus spp. are absent and I. trianguliceps is most frequent on C. rutilus (Pall.). High frequencies are, however, found also on Microtus spp. and on Neomys fodiens Penn. (II).

A characteristic feature of I. trianguliceps is that the adults are very rare on soricids.

The distribution of the two tick species in the host populations is highly clumped and fits the negative binomial distribution. A restricted part of the host population carries the majority of the ticks (II, VI, Randolph 1975 b).

The violent population fluctuations among small mammals in northern Scandinavia induce great changes in the I. trianguliceps population. The highest infestation of I. trianguliceps larvae on their hosts is obtained two years after a rodent peak (II), which indicates that the developmental cycle of I. trianguliceps in the northern part of its range may last for several years.

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References

- Arthur, D.R. 1952. Ticks collected from birds in Sweden. - Ann. Mag. nat. Hist. 5: 305-308.
- Arthur, D.R. 1955. Observations on collections of ticks from Denmark. - Ent. Meddr. 27: 76-81.
- Arthur, D.R. 1962. Ticks and disease. - Pergamon Press, Oxford.
- Balashov, Yu. S. 1968. Bloodsucking ticks (Ixodoidea) - Vectors of diseases of man and animals. - Nauka Publ., Leningrad. Transl. 500. Med. Zool. Dep. U.S. Nav. Med. Res. Unit 3. Cairo.
- Brinck, P., Svedmyr, A. and Zeipel, G. von. 1965. Migrating birds at Ottenby, Sweden as carriers of ticks and possible transmitters of tick-borne encephalitis virus. - Oikos 16: 88-99.
- Haarlov, N. 1962. Variation in the ixodid tick, Ixodes arboricola Schulze and Schlottke. - Parasitology 52: 425-439.
- Haarlov, N. 1973. The introduction into Denmark of the Kennel tick (Rhipicephalus sanguineus (Latr.)) with remarks on its reaction to different humidities. - Proc. 3. Int. Congr. Acarol., Prague 1971: 467-472.
- Lees, A.D. 1948. The sensory physiology of the sheep tick, Ixodes ricinus L. - J. Exp. Biol. 25: 145-207.
- Lees, A.D. and Milne, A. 1951. The seasonal and diurnal activities of individual sheep ticks (Ixodes ricinus L.). - Parasitology 41: 189-208.
- Mehl, R. 1970. Records of ectoparasitic insects and mites on birds and mammals in Norway. - Norw. J. Ent. 17: 109-113.
- Moorhouse, D.E. and Heath, A.C.G. 1975. Parasitism of female ticks by males of the genus Ixodes. - J. Med. Ent. 12: 571-572.
- Randolph, S.E. 1975 a. Seasonal dynamics of a host-parasite system: Ixodes trianguliceps (Acarina: Ixodidae) and its small mammal hosts. - J. Anim. Ecol. 44: 425-449.
- Randolph, S.E. 1975 b. Patterns of distribution of the tick Ixodes trianguliceps Birula on its hosts. - J. Anim. Ecol. 44: 451-474.

- Saikku, P., Ulmanen, I. and Brummer-Korvenkontio, M. 1971.
Ticks (Ixodidae) on migrating birds in Finland. - Acta
Ent. Fenn. 28: 46-51.
- Schulze, P. 1930. Erster Beitrag zu einer Zeckenfauna Schwe-
dens. - Medd. Göt. Mus. Zool. Avd. 54: 1-18.
- Tambs-Lyche, H. 1943. Notes on Norwegian ticks. - Berg. Mus.
Årbok 1943: 1-8.
- Ulmanen, I., Saikku, P., Vikberg, P. and Sorjonen, J. 1977.
Ixodes lividus (Acari) in sand martin colonies in Fenno-
scandia. - Oikos 28: 20-26.

DISTRIBUTION, HOST RELATIONS, AND SEASONAL OCCURRENCE OF *IXODES TRIANGULICEPS* BIRULA (ACARI) IN FENNOSCANDIA

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Abstract. *Ixodes trianguliceps* Birula is distributed throughout Fennoscandia and Denmark except in the northernmost parts of Norway, Sweden and Finland and in the high mountain areas of Norway and Sweden. It occurs on most species of small mammals. In woodland habitats in southern Sweden *Sorex minutus* L. is the main host of the larvae. *Clethrionomys glareolus* Schreb., especially males during the mating period in the spring, and *Apodemus flavicollis* Melch. are important to all developmental stages. 20 % — 30 % of the small mammals were infested during two yearly infestation maxima, the first in April and the second in September.

Ixodes trianguliceps Birula is a poorly known species in Fennoscandia and Denmark. Schulze (1930), Tambs-Lyche (1943), Arthur (1955), P. Brinck et al. (1967) and Ulmanen (1972) recorded it from altogether 13 areas in Denmark, Sweden, Norway and Finland. Another 73 localities are recorded in the present paper (Fig. 1). All the specimens were found on small mammals most of which were trapped alive.

I. trianguliceps is a West Palearctic species and belongs to the most cold resistant species of the genus *Ixodes* (Korenbeg and Lebedeva 1969). It infests digging small mammals and prefers humid habitats (Lichard 1965). The seasonal occurrence has been investigated in the Soviet Union (Vysotskaya 1951), Poland (Lachmajer 1962), England (Cotton and Watts 1967), Austria (Mahnert 1971) and Finland (Ulmanen 1972). *I. trianguliceps* probably plays an important role in maintaining pathogenic virus in small-mammal populations (Varma 1964).

MATERIAL

A field study was made in two woodland habitats, Kullaberg and Stampen, in southernmost Sweden in 1968—1971. Localities and collecting techniques were described by Edler and Nilsson (1973). 992 small mammals were collected in live traps and yielded 232 *I. trianguliceps*. The majority were larvae, while nymphs and adults made up 9.5 % and 11.6 % respectively. Out of 27 adult specimens, 4 were males (Fig. 2).



Fig. 1. The distribution of *Ixodes trianguliceps* in Fennoscandia and Denmark. O indicates localities where at least 20 small mammals were trapped but no *I. trianguliceps* were found. The map is based on collections at the Department of Animal Ecology, University of Lund, Schulze (1930), Tambs-Lyche (1943), Arthur (1955), Brinck et al. (1967) and Uimanen (1972). Complete lists of all the material and the collectors are deposited in the Department of Animal Ecology, University of Lund.

RESULTS

DISTRIBUTION

I. trianguliceps is distributed throughout Fennoscandia and Denmark, except in the northernmost parts of Norway, Sweden and Finland and in the high mountain areas of Norway and Sweden (Fig. 1). It seems to be absent on the islands of Bornholm and Gotland, where one of its primary hosts, *Clethrionomys glareolus*, is absent. *I. trianguliceps* exists far to the north along the Norwegian west coast. The northernmost locality known so far is 8 km SW Sortland, Langøy, Lofoten (68°40'N, 15°15'E).

HOSTS

The following small mammal species were recorded as hosts of *I. trianguliceps* in Fennoscandia and Denmark: *Sorex minutus* L., *S. araneus* L., *S. isodon* Turov, *Neomys fodiens* Penn., *Myopus schisticolor* Lillj., *Clethrionomys glareolus* Schreb., *C. rutilus* Pall., *C. rufocanus* Sund., *Microtus agrestis* L., *M. arvalis* Pall., *M. oeconomus* Pall., *Apodemus sylvaticus* L., *A. flavicollis* Melch., *Micromys minutus* Pall., *Mus musculus* L., *Mustela nivalis* f. *rixosa* L.

Numerous *S. caecutiens* Laxm. and *Lemmus lemmus* L. were examined but carried no ticks. In Scandinavia these species normally live in areas where *I. trianguliceps* does not occur.

% infested hosts

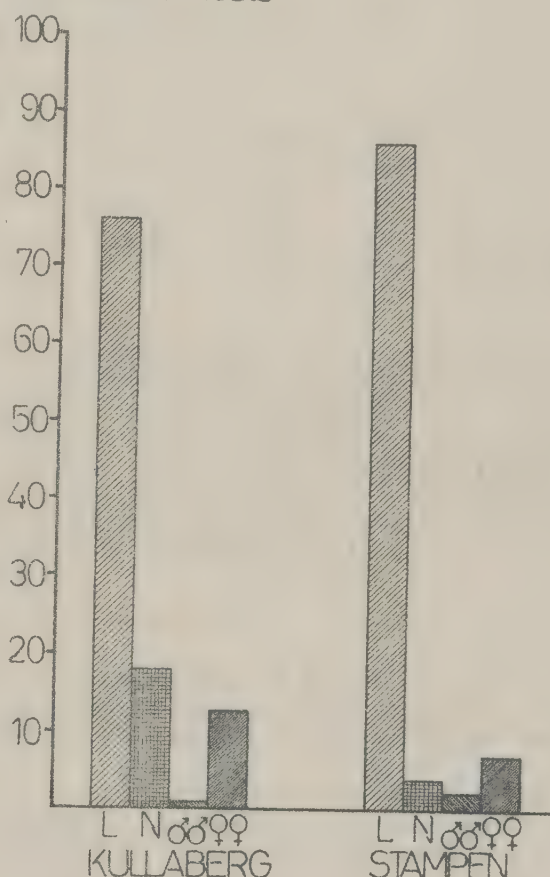


Fig. 2. Frequency distribution of stages of *Ixodes trianguliceps* on small mammals at Kullaberg and Stampen. L = larvae, N = nymphs.

HABITAT SELECTION

I. trianguliceps was found on hosts from most habitat types; in open land such as moorland, meadows, peat mosses, bogs and clearings as well as in different types of pine and deciduous forests, even in mountain birch forests in northwestern Norway.

Two main areas have been selected to show differences in host infestation in different habitats, viz. Draved in southernmost Denmark (visited in November 1971), and the river valleys Gudbrandsdalen, Österdalen and Trysiltdalen in southeastern Norway (visited in July 1967, 1968). In Draved the infestation percentage was significantly higher on the peat moss than in the forests ($t = 3.70$; $P < 0.001$). In southeastern Norway more hosts were infested in the meadows than in the pine and the deciduous forests ($t = 5.92$, $t = 5.34$; $P < 0.001$) (Tab. 1).

Table 1. Infestation of small mammals with *Ixodes trianguliceps* in various habitat types in two areas in Denmark and Norway.

	Habitat type	No. trapped	No. infested	% infested	No. ticks	Mean no. ticks	
						per host	per infested host
Draved, Denmark Nov. 1971	Deciduous forest	542	64	11.8	137	0.3	2.1
	Peat-moss	98	29	29.6	225	2.3	7.8
SE Norway July 1967, 1968	Deciduous forest	99	26	26.3	85	0.9	3.3
	Pine forest	211	64	30.3	307	1.5	4.8
	Meadow	105	64	61.0	669	6.4	10.5

In southern Finland Ulmanen (1972) found it likely that *I. trianguliceps* prefers forests and forest plantations to wet meadows and other seasonally flooded grassland. According to Lachmajer (1962) such habitats are not favourable.

Certain types of extreme habitats within the main distribution area in Fennoscandia were avoided by *I. trianguliceps* e.g. wet meadows close to sea (Skåne, Barsebäck), wet woodland (Blekinge, Almö), moorland, exposed and very dry in summers (Öland), and woodland and high mountain heath close to the tree-limit at an altitude of 800–930 m (Oppland, Skjaeringfjell and Dalarna, Långfjället) (Fig. 1).

INFESTATION OF THE HOST SPECIES (Tab. 2)

S. minutus was the most heavily infested host species (37.5 %; 2.5 ticks per individual). The infestation rate was significantly higher than in any other host species ($t = 2.79$; $0.001 < P < 0.01$). The infestation of *S. araneus* was comparatively low (9.1 %; 0.2 ticks per individual).

Among the rodents *C. glareolus* was the most infested species (13.1 %) especially by nymphs and adults. 66.7 % of all nymphs were found on *C. glareolus*. More *A. flavicollis* (10.7 %) than *A. sylvaticus* (4.8 %) were infested with *I. trianguliceps*. *A. sylvaticus* had the lowest infestation rate of all infested species ($t = 1.37$; $0.01 < P < 0.2$). A small number of *N. fodiens* and *M. agrestis* were also trapped but had no ticks. Adult ticks were found on *C. glareolus*, *A. flavicollis* and *A. sylvaticus*.

Table 2. Infestation of small-mammal species by *Ixodes trianguliceps* at Kullaberg and Stampen.
L = larvae, N = nymphs and A = adults.

Host species	No. trapped	No. infested	% infested ± mean error	No. ticks				Mean no. ticks	
				L	N	A	Total	per host	per infested host
<i>Sorex minutus</i>	32	12	37.5 ± 8.6	78	1	0	79	2.5	6.6
<i>Sorex araneus</i>	110	10	9.1 ± 2.7	22	2	0	24	0.2	2.4
<i>Neomys fodiens</i>	1	0	0	0	0	0	0	0	0
<i>Clethrionomys glareolus</i>	344	45	13.1 ± 1.8	32	16	16	64	0.2	1.4
<i>Microtus agrestis</i>	8	0	0	0	0	0	0	0	0
<i>Apodemus flavicollis</i>	309	33	10.7 ± 1.8	41	3	8	52	0.2	1.6
<i>Apodemus sylvaticus</i>	188	9	4.8 ± 1.5	10	0	3	13	0.1	1.4
Total	992	109	11.0 ± 1.0	183	22	27	232	0.2	2.1

INFESTATION IN RELATION TO SEX AND AGE OF HOST

Males of *C. glareolus* were more heavily infested than females, the difference being significant in the spring peak ($t = 2.44$; $0.01 < P < 0.05$). No such difference was found in other host species. Nor were there differences in the infestation of the age groups of the host species.

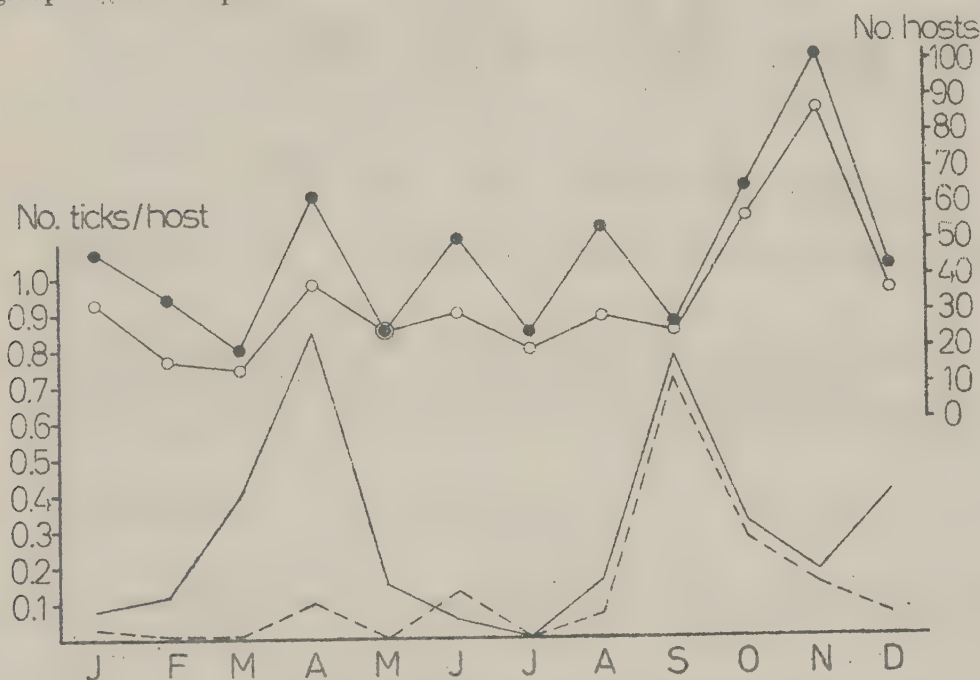


Fig. 3. Seasonal infestation of *Ixodes trianguliceps* in relation to the sex of the host. —○— = no. of ticks on male hosts. ----○---- = no. of ticks on female hosts. —●—●— = no. of investigated males. -○-○-○- = no. of investigated females.

SEASONAL CHANGES IN THE INFESTATION

The *I. trianguliceps* population was active all the year round. The infestation reached two peaks. The first was in April and the second in September. During these periods 20 % — 30 % of the small mammals were infested. In winter and in the middle of the summer the infestation was much lower. Even during the coldest part of the year a certain number of active ticks was found. The lowest infestation rate was found in July, when just one out of 49 trapped small mammals was infested (Fig. 3).

The larvae were found on the hosts throughout the year except in July. In autumn and in winter they made up 93 % of all stages, while in spring and summer the values were 58 % and 67 % respectively (Fig. 4).

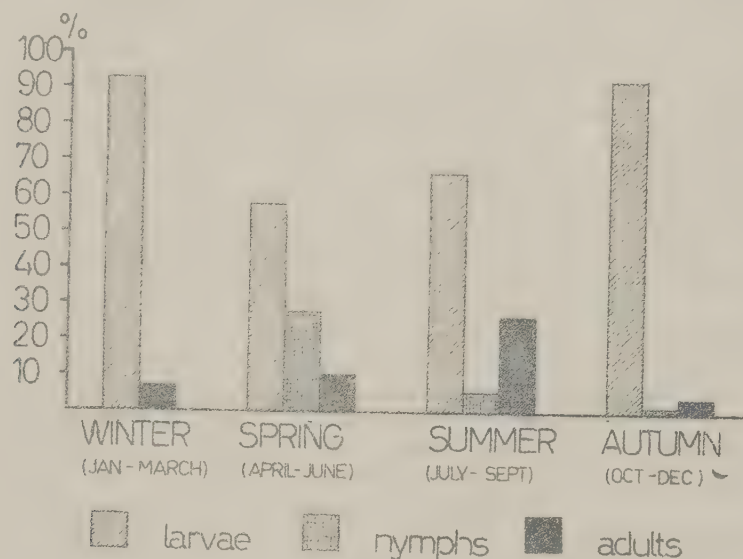


Fig. 4. Seasonal variation in relative frequency of stages of *Ixodes trianguliceps*. 100 % = all ticks in one season.

Nymphs appeared in April—June and September—October. In spring they made up 28 % of all stages. In summer and autumn they were rare (Fig. 4).

Adults were active in all seasons (Fig. 4). In the summer they constituted 27 % of the tick material. The other seasons they made up less than 11 % of all ticks.

DISCUSSION

I. trianguliceps seems to have a continuous distribution in Fennoscandia, except in the northernmost parts. In central Europe and in the Soviet Union (Lichard 1965, Nosek et al. 1967 and Lutta 1968) it has a patchy distribution preferring hilly land and mountains. In Czechoslovakia it has been recorded at altitudes of 1800 m and 2016 m in the Tatras (Černý 1972). Mahnert (1971) and Sixl (pers. comm.) found it at similar levels in Austria. In Scandinavia it is a lowland species. Its absence in the north of Fennoscandia is probably a result of the adverse climate. Its absence on the

large islands in the Baltic may be connected with the absence of the primary host species, *C. glareolus*.

The nymphs constituted a comparatively small part of the material. Probably the sucking time on the hosts is longer for the adults, making the proportion of adults on the hosts larger. The adults made up smaller part of the whole population than in the material collected off hosts.

Adult males were rare on the hosts. The reason for this is not clear. There may be less males in the population or the males may be more inclined to stay off the host (cf. Arthur 1963), being on the hosts only during the short copulation (Arthur 1962). No copulating ticks were found in this investigation. In England, however, Cotton and Watts (1967) found males and females in copula on *C. glareolus* and *M. agrestis*.

Vysotskaya (1951), Lachmajer (1962) and Arthur (1963) suggest that, when off the host, *I. trianguliceps* live in the nests or in the burrows of small mammals. Cotton and Watts (1967) examined many hundreds of nests and found both males and nymphs, however not in large numbers. It is therefore possible that *I. trianguliceps* is not confined to nests and burrows, but also lives in the surface layer of leaf litter till the infestation of small mammals. The heavy infestation of *C. glareolus* is probably due to its low ability of getting rid of the parasites (Nikitina and Zhmayeva 1963). No such investigation has been made concerning the shrew species. *S. minutus* is however more active than *S. araneus* (Croin Michielsen 1966), thus collecting more ticks. *S. minutus* is a particularly important host for the larvae, while nymphs and adults are especially abundant on *C. glareolus* but also on *A. flavicollis* (cf. Lachmajer 1962, Lutta 1968, Varma and Smith 1971). According to Ulmanen (1972), *M. agrestis* is as important a host as *C. glareolus* and *A. flavicollis* in Finland.

The heavy infestation of *C. glareolus* males during the spring maximum of the tick species coincides with the mating period of the rodent. During this period the males are more active than the females and have much larger home-ranges (Bergstedt 1966), thus collecting more ticks. Higher infestation of *I. trianguliceps* on males than on females has been reported by Nikitina (1960) and Cotton and Watts (1967). G. Brinck (1966), Brinck-Lindroth (1968) and Ulmanen and Myllimäki (1971) found similar heavy infestation of fleas on small mammals.

The seasonal occurrence of the ticks with two peaks in the year is in accordance with the findings of earlier investigations. In England (Cotton and Watts 1967) the spring peak occurred much earlier than in Poland (Lachmajer 1962), Soviet Union (Vysotskaya 1951), Finland (Ulmanen 1972) and Sweden. In Austria, Mahnert (1971) found only one peak.

In England Cotton and Watts (1967) found infestation frequencies of 50 % — 70 % during the most tick-abundant periods. In Poland (Lachmajer 1962) and Czechoslovakia (Lichard 1965) the infestations were somewhat lower. The frequencies reported by Vysotskaya (1951) in the Soviet Union and Ulmanen (1972) in Finland are close to mine.

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РАСПРОСТРАНЕНИЕ, ХОЗЯИНСКИЕ ОТНОШЕНИЯ И СЕЗОННОЕ НАЛИЧИЕ КЛЕЩА *IXODES TRIANGULICEPS* BIRULA (ACARINA) В ФЕННОСКАНДИИ

А. Нильсон

Резюме. *Ixodes trianguliceps* Birula распространен по всей территории Фенноскандии и Дании кроме самых северных частей Норвегии, Швеции и Финляндии и в высокогорных областях Норвегии и Швеции. Он паразитирует на большинстве видов мелких млекопитающих. В лесистых местностях южной Швеции главным хозяином личинок является *Sorex minutus* L. Важными хозяевами для всех стадий развития клеща являются *Clethrionomys glareolus* Schreb., особенно самцы во время весеннего периода спаривания, и *Apodemus flavicollis* Melch. 20—30 % мелких млекопитающих были заражены клещами во время двухгодичных пиков заражения, в апреле и в сентябре.

REFERENCES

- ARTHUR D. R., Observations on collections of ticks from Denmark. Ent. Medd. 27: 76—81, 1955.
- , Ticks and disease. Pergamon Press, London. 445 pp., 1962.
- , British Ticks. Butterworths, London. 213 pp., 1963.
- BERGSTEDT B., Home ranges and movements of the rodent species *Clethrionomys glareolus* (Schreber), *Apodemus flavicollis* (Melchior) and *Apodemus sylvaticus* (Linné) in southern Sweden. Oikos 17: 150—157, 1966.
- BRINCK G., Siphonaptera from small mammals in natural foci of tick-borne encephalitis virus in Sweden. Opusc. Ent. 31: 156—170, 1966.
- BRINCK P., JOHNELS A., LUNDHOLM B., SVEDMYR A., von ZEIPPEL G., ZETTERBERG B., Small mammals in Sweden as hosts of tick-borne encephalitis virus and vagrant parasites. Oikos 18: 124—134, 1967.
- BRINCK-LINDROTH G., Host spectra and distribution of fleas of small mammals in Swedish Lapland. Opusc. Ent. 33: 327—358, 1968.
- ČERNÝ V., The tick fauna of Czechoslovakia. Folia parasit. (Praha) 19: 87—92, 1972.
- COTTON M. J., WATTS C. H. S., The ecology of the tick *Ixodes trianguliceps* Birula (Arachnida: Acarina: Ixodoidea), Parasitology 57: 525—531, 1967.
- CROIN MICHELSSEN N., Intraspecific and interspecific competition in the shrews *Sorex araneus* L. and *S. minutus* L. Arch. Néerl. Zool. 17: 73—174, 1966.
- EDLER A., NILSSON A., Numerical relations between groups of ectoparasites on small mammals. Ent. Scand. 4: 274—282, 1973.
- KORENBERG E. I., LEBEDEVA N. N., Distribution and some general features of the ecology of *Ixodes trianguliceps* Bir. in the Soviet Union. Folia parasit. (Praha) 16: 143—152, 1969.
- LACHMAJER J., The ecology of the tick *Ixodes trianguliceps* Bir., 1895. Bull. Inst. Mar. Med. Gdansk 13: 149—160, 1962.
- LICHARD M., Poznámky k výskytu a ekológii kliešťa *Ixodes trianguliceps* Birula, 1895. Biológia 20: 348—358, 1965.
- LUTTA A. S., *Ixodes trianguliceps* Bir. and its distribution in Karelia. Parazitologia 2: 142—147, 1968. (In Russian.)
- MAHNERT V., Parasitologische Untersuchungen an alpinen Kleinsäugetern: Ixodoidea (Acar.). Mitt. Schw. Ent. Ges. 44: 323—332, 1971.
- NIKITINA N. A., The biology of *Ixodes trianguliceps* Bir. Med. parazitol. (Moskva) 29: 708—712, 1960. (In Russian.)
- , ZHMAYEVA Z. M., Factors determining the tick infestation rate of different host species. Med. parazitol. (Moskva) 32: 39—43, 1963. (In Russian.)
- NOSEK J., LICHARD M., SZTANKAY M., The ecology of ticks in the Tribeč and Hronský Inovec Mountains. Bull. WHO 36, Suppl. 1: 49—59, 1967.
- SCHULZE P., Erster Beitrag zu einer Zeckenfauna Schwedens. Göteborgs K. Vetensk.-o. Vitterh Samh. Handl., 5.F., ser. B1 13: 1—18, 1930.
- TAMBS-LYCHE H., Notes on Norwegian ticks. Bergens Mus. Årbok 3: 1—8, 1943.
- ULMANEN I., Distribution and ecology of *Ixodes trianguliceps* Birula (Acarina, Ixodoidea) in Finland. Ann. Zool. Fennici 9: 111—115, 1972.
- , MYLLIMÄKI A., Species composition and

- number of fleas (Siphonaptera) in a local population of the field vole, *Microtus agrestis* (L.). Ann. Zool. Fennici 8: 374—384, 1971.
- VARMA M. G. R., The acarology of louping ill. Acarologia fasc. h. s., 1964.
- , SMITH C. E. G., The epidemiology of louping ill in Ayrshire, Scotland — II. Ectoparasites of small mammals (Ixodoidea). Folia parasit. (Praha) 18: 63—72, 1971.
- VYSOTSKAYA S. O., On the biology of *Ixodes trianguliceps* Bir. Parazitol. Sbornik 13: 105—110, 1951. (In Russian.)

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Host relations and population changes of *Ixodes trianguliceps* (Acari) in northern Scandinavia

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Near its northern limit *Ixodes trianguliceps* Birula prefers woodland habitats where it mainly infests the rodents *Clethrionomys rutilus* Pall. and *Microtus agrestis* L., and the shrew *Neomys fodiens* Penn. Male *Clethrionomys* species are more infested than females. The annual abundance, especially of larvae, varies inversely with the population densities of *C. rutilus* and *M. agrestis*.

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У северных пределов ареала *Ixodes trianguliceps* Билуло предпочитает лесные местообитания, где они преимущественно паразитируют на грызунах *Clethrionomys rutilus* Pall и *Microtus agrestis* L. и землеройках *Neomys fodiens* Penn. Самцы *Clethrionomys* заражаются сильнее, чем самки. Наблюдается инверсия сезонного обилия, особенно нимф, в сравнении с плотностью популяций *C. rutilus* и *M. agrestis*.

1. Introduction

This study is part of an investigation on the dynamics, host relations and habitats of ectoparasites of small mammals in northern Scandinavia and Finland. It examines the *Ixodes trianguliceps* Birula population of the Lofoten area in northwestern Norway, which is the northernmost area known for the species (Nilsson 1974). The area has a humid climate which is favourable for *I. trianguliceps* (Lachmajer 1962). This is the only tick occurring on rodents this far north.

Hosts were collected in late July to early September every year from 1965 to 1970 by live-trapping in woodland and open habitats. Collecting techniques were described by Andersson and Hansson (1966) and Edler and Nilsson (1973).

2. Material

3860 small mammals were collected in live traps and yielded 2123 *I. trianguliceps* (Tab. 1). Most were larvae (64.0%). Nymphs and adults made up 31.1% and 4.9% respectively. Only 16 males were found, all except one on hosts also infested with female ticks. A pair was found in copula on one *Clethrionomys rutilus*.

3. Results

3.1. Habitats

The study area was divided into two main habitats. These were woodland with mountain birch forests and open habitats such as meadows and bogs. Small mammals from woodland areas had a much higher infestation rate (18.0%) than those trapped in open habitats (0.6%).

3.2. Infestation of hosts

Hosts from the different habitats were not considered separately. Only a few small mammals were collected

from open habitats and these did not significantly influence the results.

C. rutilus (Tab. 1) was the most heavily infested host (47.2%, 2.5 ticks per specimen, $t = 2.92$, $0.01 > P > 0.001$). *Microtus oeconomus* also showed high infestation but only two individuals were caught. *C. rufocanus* had a very low infestation (3.2%, 0.1 ticks per specimen). *M. agrestis* which lives in woodlands in northern Scandinavia had an infestation rate of 31.6% (0.8 ticks per specimen). This is significantly higher than in *Sorex araneus* (16.5%, 0.5 ticks per specimen, $t = 4.35$, $P < 0.001$) and *S. minutus* (11.8%, 0.5 ticks per specimen, $t = 2.32$, $0.05 > P > 0.01$). Among the soricids *Neomys fodiens* was the most infested species (39.3%, 1.7 ticks per specimen) and was significantly more infested than *S. araneus* ($t = 2.47$, $0.05 > P > 0.01$) and *S. minutus* ($t = 2.19$, $0.05 > P > 0.01$). Almost all *Mus musculus* were trapped in one locality in 1965. Infestation was slight at 6.5% and 0.1 ticks per specimen. A few *Lemmus lemmus* were trapped but carried no ticks. Most of the ticks infesting *N. fodiens*, *C. rutilus* and *M. agrestis* were postlarval stages: 40.8%, 49.2% and 85.9% respectively (Tab. 4). Adult ticks were found on *S. araneus* (2), *C. rutilus* (58), *C. rufocanus* (1) and *M. agrestis* (43).

The frequency distribution of ticks on *C. rutilus* and *S. araneus* differed considerably. More *C. rutilus* carried a large number of ticks, particularly nymphs, and only 0.9% of the *S. araneus* population had more than 2 ticks. The corresponding value for *C. rutilus* was 18.5% (Fig. 1).

Multiple infestation by *I. trianguliceps* was common. Among *S. araneus* 32.1% had 3 or more ticks. Corresponding values for *C. rutilus* and *M. agrestis* were 54.4% and 25.5% respectively.

Some times there was a high number of ticks on a host. Thus 24 *S. araneus*, 10 *C. rutilus* and 2 *M. agrestis* each carried 10 or more ticks. One *C. rutilus* had 44 *I. trianguliceps*. The individual maximum on *S. araneus* was 36 ticks (Tab. 1).

Tab. 1. Infestation of small mammal species with *Ixodes trianguliceps*.

	No. hosts	No. infested hosts	% infested hosts	No. ticks	No. ticks/ host	No. ticks/infested host	Individ. maximum
<i>Sorex araneus</i> L.	3178	524	16.5	1533	0.5	2.9	36
<i>S. minutus</i> L.	17	2	11.8	8	0.5	4.0	7
<i>Sorex</i> sp.	2	—	—	—	—	—	—
<i>Neomys fodiens</i> Penn.	28	11	39.3	50	1.8	4.6	8
<i>Lemmus lemmus</i> L.	4	—	—	—	—	—	—
<i>Clethrionomys rutilus</i> Pall.	144	68	47.2	355	2.5	5.2	44
<i>C. rufocanus</i> Sund.	221	7	3.2	16	0.1	2.3	7
<i>Microtus agrestis</i>	187	59	31.6	145	0.8	2.5	23
<i>M. oeconomus</i> Pall.	2	2	100.0	7	3.5	3.5	4
<i>Mus musculus</i> L.	77	5	6.5	9	0.1	1.8	5
Total.	3860	678	18.3	2123	0.5	3.1	44

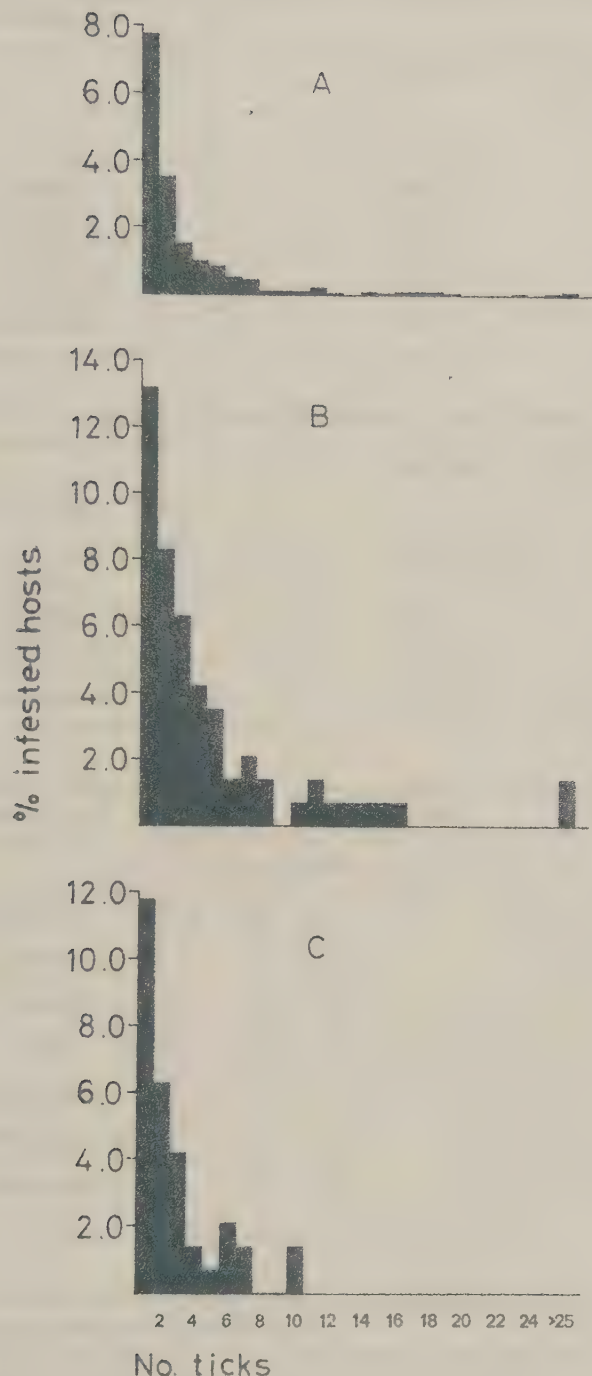


Fig. 1. Frequencies of *Ixodes trianguliceps* on (A) *Sorex araneus* (n = 3178), (B) *Clethrionomys rutilus* (n = 144), and (C) *C. rutilus* (nymphs only).

3.3. Infestation in relation to age and sex of host

Immature *S. araneus* had a significantly higher infestation rate than adults ($t = 10.71$, $P < 0.001$). Among *C. rutilus* and *C. rufocanus* adults were more infested

than juveniles ($t = 3.67$, $P < 0.001$; $t = 2.77$, $0.01 > P > 0.001$, respectively). In the other species there was no such difference (Tab. 2).

Significant differences in the infestation rate between sexes was found only in *C. rutilus* and *C. rufocanus*, where males were more infested than females ($t = 2.26$, $0.05 > P > 0.01$; $t = 2.12$, $0.05 > P > 0.01$) (Tab. 3). In *C. rutilus* the difference was significant for all developmental stages (larvae: $t = 3.54$, $0.01 > P > 0.001$; nymphs: $t = 2.45$, $0.05 > P > 0.01$; males: $t = 2.31$, $0.05 > P > 0.01$; females: $t = 2.87$, $0.01 > P > 0.001$) (Tab. 4).

C. rutilus males appear to be important hosts of adult *I. trianguliceps* ($t = 1.76$, $0.05 > P > 0.01$). Of all adult ticks found on *C. rutilus* all male ticks and 42 (87.5%) females occurred on male hosts. The individual carrying most adult ticks (5 ♂♂ and 10 ♀♀) was a young female *M. agrestis*.

3.4. Annual changes in infestation

The infestation rate of *I. trianguliceps* varied between the sampling years. For *C. rutilus* it was 27.6% in 1970 and 63.4% in 1966, for *M. agrestis* 9.4% in 1970 and 63.6% in 1968 and for *S. araneus* 8.9% in 1969 and 23.7% in 1968.

Similarly the number of ticks per host varied. For *C. rutilus* it was 1.0 in 1970 and 6.9 in 1968, for *M. agrestis* 0.1 in 1970 and 2.7 in 1968, and for *S. araneus* 0.1 in 1969 and 1.1 in 1968 (Fig. 2).

Ticks were particularly numerous on *C. rutilus* and *M. agrestis* in years of low population densities of these species. In years when *C. rutilus* and *M. agrestis* had high population densities the number of ticks per host, particularly larvae, was low. The annual variation in numbers per host was small among nymphs and adults, especially in *C. rutilus* and *S. araneus* (Fig. 2).

The larval part of the host-bound tick population gradually increased from 1966 to 1968 when they constituted 88.9%. The following year they were few (11.8%), while nymphs and adults made up a major part (Fig. 3).

4. Discussion

In contrast to conditions in southern Scandinavia (Nilsson 1974), hosts from woodland areas were much more infested than hosts trapped in open habitats. Similar results were reported from the Soviet Union (Vysotskaya 1951, Nikitina 1960), Poland (Lachmajer 1962) and southern Finland (Ulmanen 1972). In England, however, the host habitat seems to be unimportant for the occurrence of *I. trianguliceps* on small mammals (O'Donnell 1973).

The infestation of the small mammal population was about the same in 1965–1970 (Tab. 1) as in the Soviet Union (Vysotskaya 1951), Poland (Lachmajer 1962) and southern Finland (Ulmanen 1972). In England

Tab. 2. Infestation of (A) juveniles (pre-adults among soricids) and (B) adults of small mammal species with *Ixodes trianguliceps*.

	No. hosts		No. infested hosts		% infested hosts		No. ticks		No. ticks/ host		No. ticks/ infested host	
	A	B	A	B	A	B	A	B	A	B	A	B
<i>S. araneus</i>	2796	311	500	12	17.9	3.9	1485	20	0.5	0.1	3.0	1.7
<i>S. minutus</i>	12	5	1	1	8.3	20.0	1	7	0.1	1.4	1.0	7.0
<i>N. fodiens</i>	21	6	8	2	38.1	33.3	38	11	1.8	1.8	4.6	5.5
<i>C. rutilus</i>	28	82	5	42	17.9	51.2	27	253	1.0	3.1	5.4	6.0
<i>C. rufocanus</i>	108	82	—	7	—	8.5	—	16	—	0.2	—	2.3
<i>M. agrestis</i>	76	86	24	26	31.6	30.2	49	79	0.6	0.9	2.0	3.0
<i>M. musculus</i>	39	34	2	3	5.1	8.8	2	7	0.1	0.2	1.0	2.3

Tab. 3. Infestation of males and females of small mammal species with *Ixodes trianguliceps*.

Sex of host	No. hosts		No. infested hosts		% infested hosts		No. ticks		No. ticks/ host		No. ticks/ infested host	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
<i>S. araneus</i>	1514	1268	254	240	16.8	18.9	711	734	0.5	0.6	2.8	3.1
<i>S. minutus</i>	7	9	2	—	28.6	—	8	—	1.1	—	4.0	—
<i>N. fodiens</i>	16	11	5	5	31.3	45.5	30	19	1.9	1.7	6.0	3.8
<i>C. rutilus</i>	85	59	48	20	56.5	33.9	320	35	3.8	0.6	6.7	1.8
<i>C. rufocanus</i>	94	127	6	1	6.4	0.8	15	1	0.2	0.0	2.5	1.0
<i>M. agrestis</i>	85	102	29	30	34.1	29.4	76	69	0.9	0.7	2.6	2.3
<i>M. musculus</i>	37	40	4	1	10.8	2.5	8	1	0.2	0.0	2.0	1.0

Tab. 4. Distribution of developmental stages of *Ixodes trianguliceps* in relation to the host and its sex.

		Larvae		Nymphs		♂	♀	Total
<i>S. araneus</i>	♂ (1514)	514	196	—	1	—	1	711
	♀ (1268)	510	223	1	—	—	—	734
<i>S. minutus</i>	♂ (7)	8	—	—	—	—	—	8
	♀ (9)	—	—	—	—	—	—	—
<i>N. fodiens</i>	♂ (16)	15	15	—	—	—	—	30
	♀ (11)	14	5	—	—	—	—	19
<i>C. rutilus</i>	♂ (85)	169	102	7	42	—	—	320
	♀ (59)	13	16	—	6	—	—	35
<i>C. rufocanus</i>	♂ (94)	11	3	—	1	—	—	15
	♀ (127)	—	1	—	—	—	—	1
<i>M. agrestis</i>	♂ (85)	26	34	1	15	—	—	76
	♀ (102)	18	24	7	20	—	—	69
<i>M. musculus</i>	♂ (37)	6	2	—	—	—	—	8
	♀ (40)	1	—	—	—	—	—	1

(Cotton and Watts 1967) and Austria (Mahnert 1971) the infestation rates were higher.

The wide small mammal host range for *I. trianguliceps* noted in this study was similar to other investigations (Korenberg and Lebedeva 1969, Nilsson 1974), although the infestation rate differed very much between the various small mammals species. *C. rutilus*, *M. agrestis* and *N. fodiens* showed much the highest infestation rates. *M. agrestis* is known to be an important host of *I. trianguliceps* (Ulmanen 1972, O'Donnell 1973), while this is new for *C. rutilus*. As regards *N. fodiens*, Katelina et al. (1973) found in the Tula region of the Soviet

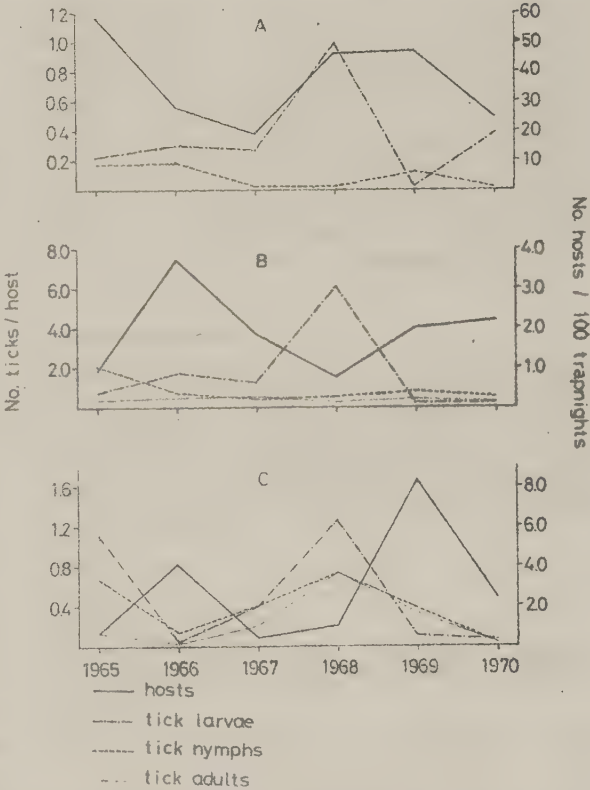


Fig. 2. Population density of *Ixodes trianguliceps* in relation to population densities of (A) *Sorex araneus*, (B) *Clethrionomys rutilus* and (C) *Microtus agrestis*.

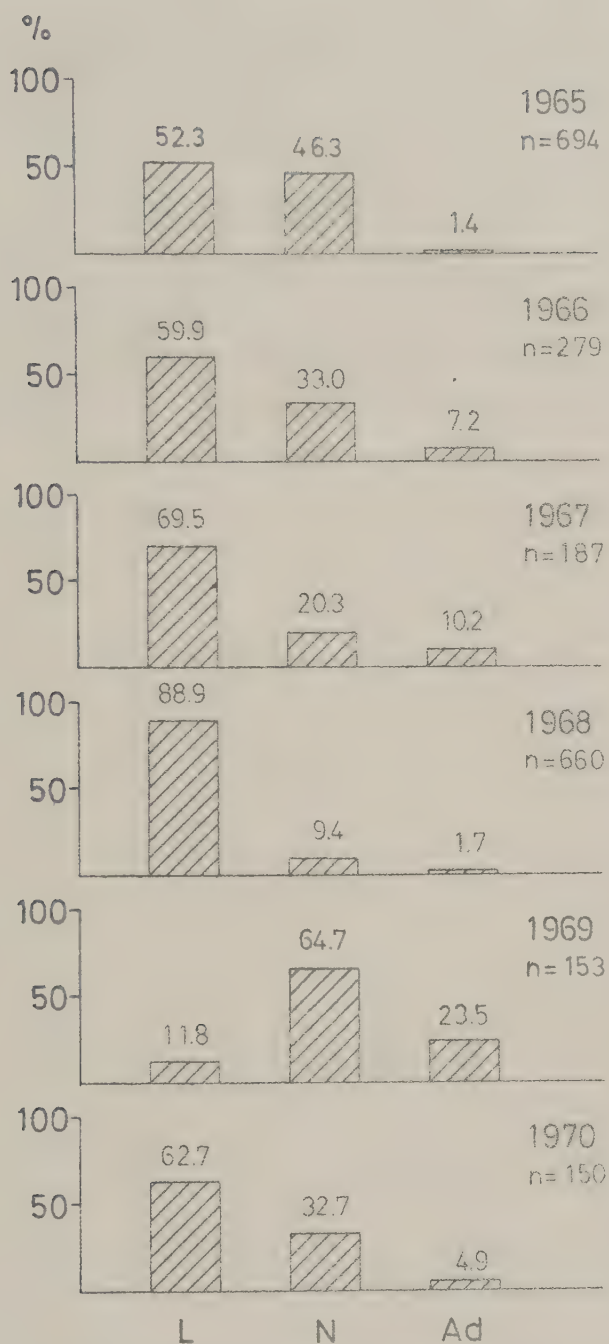


Fig. 3. Distribution of development stages of *Ixodes trianguliceps* in 1965–1970. L = larvae, N = nymphs, Ad = adults.

Union more *I. trianguliceps* on *N. fodiens* than on other hosts, though less than in the present study. This may have been due to the low abundance of *I. trianguliceps* in their investigation area. Infestation of *C. rufocanus* was remarkably small due to a low abundance of ticks in the locality where *C. rufocanus* was most numerous.

The importance of *C. rufocanus* as a host is evident from the high infestation rates (53.3%) found in south-eastern Norway (Brinck-Lindroth et al. unpubl.). The reason for the heavy infestation of non-adult *S. araneus* is not clear.

In northern Scandinavia *C. rutilus* and *C. glareolus* prefer the same habitats (Steven 1955) and seem to occupy much the same ecological niche. As hosts of *I. trianguliceps* they substitute each other in areas where only one of them occurs. Thus *I. trianguliceps*, particularly the postlarval stages, appears to be highly dependent on the presence of male *C. rutilus* and male *C. glareolus* (Cotton and Watts 1967, Nilsson 1974. See also Tab. 4). Also in the different sexes of *C. rufocanus* there was a significant difference in the infestation.

These results, together with information cited in the above literature, suggest that *I. trianguliceps* infests males of the genus *Clethrionomys* more than females. The reason is unknown.

There was great variation in annual infestation rates. Some years more than 60% of *C. rutilus* and *M. agrestis* were infested. This is similar to reports by Cotton and Watts (1967) from England during the autumn peak.

The abundance of *I. trianguliceps*, especially larvae, varied inversely with the population density of *C. rutilus* and *M. agrestis*. Katelina et al. (1973) explained similar relations between *I. trianguliceps* and *C. glareolus* in the Soviet Union as a lag in the rate of tick reproduction in relation to host reproduction. In agreement with this explanation the peaks of *C. rutilus* and *M. agrestis* populations in 1966 were followed by an increasing abundance, especially of larvae, which reached its peak two years later. Such a long lag between reproduction and larval activity suggests that the developmental cycle for this species may last for several years (Nosek et al. 1967) with a mean of less than one generation a year.

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References

- ANDERSSON, Å. and HANSSON, L. 1966. Smådäggdjursundersökningar i norra Norge 1965. – Fauna Flora 2–3: 49–72.
- COTTON, M. J. and WATTS, C. H. S. 1967. The ecology of the tick *Ixodes trianguliceps* Birula (Arachnida; Acarina; Ixodoidea). – Parasitology 57: 525–531.
- EDLER, A. and NILSSON, A. 1973. Numerical relations between groups of ectoparasites infesting small mammals. – Ent. Scand. 4: 274–282.
- KATELINA, A. F., MYASNIKOV, YU. A. and PANINA, T. V. 1973. Burrow tick *Ixodes trianguliceps* in natural foci of

- haemorrhagic fever with renal syndrome in broad-leaved forests of eastern Europe. – In: Daniel, M. and Rosický, B. (ed.). Proc. 3rd Int. Congr. Acarol. Prague 1971, pp. 603–607.
- KORENBERG, E. I. and LEBEDEV, N. N. 1969. Distribution and some general features of the ecology of the *Ixodes trianguliceps* Bir. in the Soviet Union. – Folia parasitol. 16: 143–152.
- LACHMAJER, J. 1962. The ecology of the tick *Ixodes trianguliceps* Bir., 1895. – Bull. Inst. Mar. Med. Gdansk 13: 149–160.
- MAHNERT, V. Parasitologische Untersuchungen an alpinen Kleinsäugern: Ixodoidea (Acari). – Mitt. Schw. Ent. Ges. 44: 323–332.
- NIKITINA, N. A. 1960. The biology of *Ixodes trianguliceps*. – Med. Parazitol. 6: 708–712 (In russian with english summary).
- NILSSON, A. 1974. Distribution, host relations, and seasonal occurrence of *Ixodes trianguliceps* Birula (Acarina) in Fennoscandia. – Folia parasitol. (In press).
- NOSEK, J., LICHARD, M. and SZTANKAY, M. 1967. The ecology of ticks in the Tribeš and Hronský Inovec Mountains. – Bull. Wld. Hlth Org. 36, Suppl. 1: 49–59.
- O'DONNELL, T. G. 1973. Density and host relations of *Ixodes trianguliceps* Bir. in woodland and grassland areas. – In: Daniel, M. and Rosický, B. (ed.). Proc. 3rd Int. Congr. Acarol., Prague 1971, pp. 783–787.
- STEVEN, D. M. 1955. Small mammal communities of the north Scandinavian birch forest. – J. Anim. Ecol. 24: 403–411.
- ULMANEN, I. 1972. Distribution and ecology of *Ixodes trianguliceps* Birula (Acarina, Ixodoidea) in Finland. – Ann. Zool. Fenn. 9: 111–115.
- VYSOTSKAYA, S. O. 1951. On the biology of *Ixodes trianguliceps* Bir. – Parazitol. Sbornik 13: 105–110. (In russian).

Seasonal occurrence of *Ixodes ricinus* (Acari) in southern Sweden.

by Anders Nilsson

Abstract

The seasonal occurrence of *Ixodes ricinus* L. was studied in woodland localities, on the coast and inland. Two methods were used. The blanket method provided all developmental stages, but small mammals yielded more larvae. Bimodal seasonal occurrence was found for the larvae, with spring peaks in May - June at the inland localities and about one month earlier on the coast. The autumn peak of the larvae occurred in September. Nymphal activity usually starts somewhat earlier in spring than that of the larvae. Adults had three peaks of activity - in spring, summer and autumn.

1. Introduction

Ixodes ricinus L. is a common tick species in southern Fennoscandia (Tambs-Lyche 1943, Öhman 1961, Brinck-Lindroth et al. 1975). It infests a great variety of vertebrate species, e.g. lizards, birds and terrestrial mammals (Schulze 1929, 1930, Johnsen 1946, Arthur 1952, 1955, Brinck et al. 1965, 1967, Saikku et al. 1971, Mehl 1972 a, b, c, Brinck-Lindroth et al. 1975). In certain areas I. ricinus acts as a vector of e.g. tick-borne encephalitis (TBE) and piroplasmosis (Tambs-Lyche 1943, Saikku and Brummer-Korvenkontio 1975, Traavik and Mehl 1975). In Fennoscandia the seasonal occurrence of I. ricinus has been studied by Tambs-Lyche (1943) and Brummer-Korvenkontio (1966).

In this investigation the seasonal occurrence of I. ricinus has been examined primarily in two localities in southern Sweden. Notes on small mammal ectoparasites from these areas have been published previously (Edler 1972, 1973, Edler and Nilsson 1973, Nilsson 1974, Brinck-Lindroth et al. 1975).

The seasonal occurrence of I. ricinus in the vegetation and on the hosts is regulated by egg, larval and nymphal diapauses, which delay the development. The diapauses are influenced by daylength and temperature (see Balashov 1968). The amplitude and duration of the activity peaks are most probably influenced by temperature and R.H. (cf. Macleod 1939, Milne 1945) as well as the availability of unfed ticks in the vegetation (Lees and Milne 1951). This availability is influenced by the initial abundance of unfed ticks and also by the abundance of suitable hosts which continuously remove unfed active ticks from the vegetation.

2. Material and methods

2.1. Seasonality

2.1.1. Unfed ticks in the vegetation

Ticks were collected using the blanket method (cf. e.g. Loew et al. 1963). At Kullaberg, the collections were made about once a month during May through November 1968-1970. Except for a few occasions, when adverse weather disturbed sampling, ten samples were taken from randomly chosen areas of 25 m². In 1976 at Övedskloster, the ticks were collected on each sampling occasion from one randomly chosen area of 200 m². At this locality, sampling was performed with intervals of 1 - 32 days. The blanket method provided 12,455 specimens of I. ricinus at Kullaberg and 927 at Övedskloster. The distribution between the developmental stages is shown in Tab. 1.

2.1.2. Ticks on small mammals

Collections of small mammals were made in two areas: Stampen and Kullaberg in southernmost Sweden. Trapping was performed monthly throughout the year from November 1968 through April 1971 in Kullaberg and from March 1968 through December 1969 at Stampen. An index method was used: Two multiple-catching live-traps were placed at each trapping station with the stations 15 m apart along a trap line (cf. Hansson 1967). The traps were set about 1700 and the catch removed about 0900 next day. The density of small mammals varied considerably during the investigation period in Kullaberg and the majority of hosts were collected in 1969. At Stampen there was less variation in abundance (Fig. 1). The most abundant species in Kullaberg were Clethrionomys glareolus Schreber and Apodemus sylvaticus L. and at Stampen C. glareolus and A. flavicollis Melchior.

Trapped mammals were placed in polythene bags, killed with diethyl ether and then preserved in a mixture of equal amounts of 80 % ethyl alcohol and 4 % formic aldehyde (water solution). This mixture was also injected into the peritoneal cavity of the animals. In the laboratory the ectoparasites were removed with tweezers and preserved in 80 % ethyl alcohol. A total of

2,448 specimens of I. ricinus were found on 540 small mammals at Kullaberg. At Stampen 461 hosts were infested by 887 I. ricinus. Only 47 nymphs and 1 ♀ were found; the rest were larvae.

2.1.3. Ticks in a selection of biotopes

A series of biotopes for I. ricinus containing habitats suitable for the study of the seasonality of the ticks were investigated. The infestation frequencies were calculated for ticks on small mammals trapped in grasslands and various types of woodlands (see below and Fig. 2). Trapping was performed in May and November in the Kullaberg peninsula, within a restricted area close to the sea. The 794 hosts yielded 5,188 specimens of I. ricinus.

A. and B. Two oak forests on different parts of the peninsula. They were very much alike and one of them was selected for the study of seasonality. The vegetation description below is valid for both areas.

C. Oak forest on cliffs close to the sea. Very dense and low wind-pressed (1-3 m) Quercus petraea Mattuschka with Rubus sp., Lonicera periclymenum L. and Prunus spinosus L. Grasses, Achillea millefolium L., Sorbus aucuparia L., Ranunculus ficaria L., Saxifraga granulata L. and Galium aparine L. were present in small clearings in the wood.

D. Alder forest. Mixed forest dominated by Alnus glutinosa (L.) Gaertn. with Betula pubescens Ehrh. and Sorbus aucuparia and in the bush layer Sambucus nigra L. The field layer was dense, dominated by Rubus idaeus L. and with Urtica dioica L. and ferns in places. Grasses and sedges were frequent.

E. Pine forest. Pinus silvestris L. on top of the hills. The very dense bush layer consisted primarily of Juniperus communis L. Large ferns and L. periclymenum were common.

F. Pine forest. Less dense than the former. P. silvestris with B. pubescens and S. aucuparia in places. J. communis was common. The field layer consisted of grasses, Vaccinium myrtillus L. and Convallaria majalis L.

G. Juniper. Restricted area between the cliff edges and the oak forest. J. communis, P. spinosus, Rubus sp., Rosa sp., S. aucuparia, C. majalis, Polygonatum odoratum (Mill.), Poa nemoralis L. and ferns dominated the bush and field layers.

H. Ecotones. Between oak and beech forests and grassland. P. spinosus was abundant.

I and K. Grassland. Deschampsia caespitosa (L.) with Taraxacum vulgare L., R. ficaria and Primula veris (L.) Huds. in places.

3. Study area

Kullaberg is a rocky promontory jutting into the sea. The climate is maritime: during the investigation period the monthly mean temperatures for the coldest and warmest months were -4.5°C and 17.9°C , respectively. The area, where the present investigation was performed is situated on a south slope facing the sea. The slope is covered with Q. petrea with a well developed field layer, in places luxuriant. Anemone sp., C. majalis L., P. nemoralis and L. periclymenum are typical for the area, with Hedera helix L. in places.

At Stampen, 20 km from the nearest coast, the forest is dominated by Fagus sylvatica (L.) Gaertn. Around a small stream running through the area, A. glutinosa and Q. robur L. form a rather dense forest with bushes of Corylus avellana L. and Rosa sp. Along the stream, where much of the trapping was performed, the field layer was dominated by Petasites albus (L.) Gaertn. and U. dioica. The climate has an inland character with colder winters and somewhat warmer summers. Spring is later than at Kullaberg and frosts occur early in autumn.

At Övedskloster sampling was performed in a rather young forest of Fraxinus excelsior L. with a dense canopy. The field layer was sparse with grasses, orchids, R. acris and G. aparine as dominants.

4. Results

For two representative localities the infestation frequency and number of ticks on the small mammals were calculated in order to show the seasonality of the ticks (Fig. 3). I. ricinus had a bimodal seasonal occurrence with one peak in spring or early summer and the other in autumn. Tick activity was almost zero in winter (December - March). In some years, however, a few small mammal specimens were infested even during winter season. In April, tick activity increased to a peak in May in Kullaberg and in June at Stampen. The autumn peak occurred about the same time (September) in both localities. Significant differences in infestation frequencies were found during the peaks at Stampen as well as in Kullaberg (Tab. 2). The density on the hosts varied considerably, ranging 0 - 299 at one sampling occasion.

This pattern actually reflects the activity of I. ricinus larvae. Nymphs and adults found on the hosts comprised only 1.4 % of all ticks. The seasonality of these developmental stages was studied monthly at Kullaberg with the blanket method during three years (Fig. 4). The data showed a less regular pattern than those found on the host.

For larvae no pronounced bimodality was found, except in 1969, when there were spring as well as autumn peaks. The distribution of the ticks on the ground was, however, extremely patchy (cf. SE-values) and no statistical significance was found.

For the nymphs the activity pattern was more regular, with spring peaks in May - June (in 1970 perhaps somewhat later) and the autumn peaks in October. The pattern for nymphs in 1969 was very much like that for the larvae.

The adults from the different years were pooled. Significant peaks were found in spring ($t = 10.32$; $P < 0.001$), summer ($t = 6.09$; $P < 0.001$) and autumn ($t = 3.64$; $0.01 > P > 0.001$) (Fig. 5).

An additional sampling was made at another locality, Övedskloster. A clear bimodality was observed for larvae as

well as for nymphs. The spring peak was pronounced and occurred in late May and early June (Fig. 6).

Sampling at Övedskloster was performed with closer intervals. This showed that activity can vary considerably within a very short period, as is demonstrated, for example, by the rapid decrease in larval activity in June. As at Stampen, the peak at Övedskloster was higher in spring than in autumn. The opposite was found for Kullaberg (Fig. 3).

The activity of nymphs in spring was greater than the larval activity (although in 1970 it was similar) while in autumn the opposite was found. The nymphs are active earlier in spring than the larvae. In pooled data from Kullaberg in May (a period of increasing activity in ticks) the relation between nymphs and larvae was 9.5:1 and at Övedskloster 5.6:1, while corresponding values for October (a period of decreasing activity) were 0.5:1 and 0.9:1. The same trend was found for nymphs even though they are rarely found on small mammal hosts. Thus corresponding ratios in May and October were 0.09:1 and 0.03:1 at Stampen and 0.011:1 and 0.007:1 in Kullaberg.

5. Discussion

The blanket method provided all developmental stages. Adult ticks differed from the expected bimodal occurrence (see Arthur 1962) and showed three significant peaks, despite the fact that only 224 specimens were obtained. The three peaks are not a function of the pooled data. The same trend was found for two of the three investigation years. Similarly, Mermod et al. (1974) in Switzerland did not find distinct bimodality for adult ticks. Their results were, however, not consistent with mine. In Finland Brummer-Korvenkontio (1966) found a monophasic activity in adult females, which was supported by the occurrence of piroplasmosis.

Nymphs, on the other hand, showed a displayed bimodal activity. The SE-values for nymphs were also comparatively small at least compared with the values for the larvae. The distribution of the larvae in the vegetation was extremely clumped.

Thus, on one occasion the range between samples was 11 - 562 and in another 4 - 347. This is caused by the behaviour of the engorged female, who places all her eggs in a single pile (800 - 5000 eggs, $\bar{x}$ = 2,500; Honzakova et al. 1975). The larvae tend to gather (Arthur 1962) and they do not migrate far from their place of birth (Cerný 1959).

The dispersal of ticks is thus mainly caused by the hosts and, therefore, the aggregation of unfed nymphs and adults is less than in the larvae.

Samples from hosts seem to provide better results when analysing seasonal occurrence, at least for the larvae. Even if the variation in infestation between host individuals is considerable (Nilsson and Lundqvist in ms), there is a buffering effect against sudden drops in tick activity, caused, for example, by rapid weather changes. The large area covered by the hosts also buffers against larval patchiness in the vegetation, as was shown by the results obtained using the blanket method.

The time of the autumn peak does not seem to vary much between different areas in Europe. In Wales (Edwards and Arthur 1947), Austria (Loew et al. 1963, Pretzmann et al. 1964), Switzerland (Mermod et al. 1973) and Finland (Brummer-Korvenkontio 1966) the larval peaks mostly occur in September, with few abbreviations. The onset of larval activity in spring is earlier in a more maritime area (Kullaberg) than in the inland localities. This is probably caused by delayed development of overwintered ticks in spring (see Balashov 1968).

The activity pattern differed between years. Thus, nymphs in two of the three years showed pronounced peaks of activity in late June or early July, while this activity was absent the third year. Such an irregular occurrence seems rather common for I. ricinus (Černý 1957). Edwards and Arthur (1947) stated that autumn peaks were absent in nymphs in certain years. Babenko (1973) suggested this absence to be characteristic for the northern distributional range of I. ricinus, where the suitable period for activation of newly moulted nymphs in certain years might be too short. This view was not supported

by the present study, where the autumn peak was the most consistent and there was a greater variation in spring activity between years. These variations in activity, which may be related to abundance, may also be caused by differences in host availability. In host specific ticks such as I. trianguliceps Birula (specific on burrowing small mammals) host abundance is a major factor controlling population dynamics (Nikitina 1960, Nilsson 1974). However, because I. ricinus is more catholic in its feeding habits (cf. Arthur 1963), it is less affected by population fluctuations in a single category of host species.

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References

- Arthur, D.R. 1952. Ticks collected from birds in Sweden. - Ann. Mag. Hist. Zool. Bot. Geol. 12th ser. Vol. 5.
- Arthur, D.R. 1955. Observations on collections from Denmark. - Ent. Meddr. 27: 76-81.
- Arthur, D.R. 1962. Ticks and disease. - Pergamon Press, Oxford. 445 pp.
- Arthur, D.R. 1963. British ticks. - Butterworths, London. 214 pp.
- Babenko, L.V. 1973. On the ecology of *Ixodes ricinus* L. nymphs (Ixodidae). - Proc. 3rd Int. Congr. Acarol., Prague 1971: 451-457.
- Balashov, Yu. S. 1968. Bloodsucking ticks (Ixodoidea) - vectors of diseases of man and animals. - Nauka Publishers, Leningrad. (In Russian). Transl. 500, Medical Zoology Department, U.S. Naval Medical Research Unit No. 3. Hoogstraal, H. and Tatchell, R.J. (eds.), Cairo, Egypt. 1972.
- Brinck, P., Svedmyr, A. and Zeipel, G. von. 1965. Migrating birds at Ottenby, Sweden as carriers of ticks and possible transmitters of tick-borne encephalitis virus. - Oikos 16: 88-99.
- Brinck, P., Johnels, A., Lundholm, B., Svedmyr, A., Zeipel, G. von and Zetterström, B. 1967. Small mammals in Sweden as hosts of tick-borne encephalitis virus and vagrant parasites. - Oikos 18: 124-134.
- Brinck-Lindroth, G., Edler, A., Lundqvist, L. and Nilsson, A. 1975. Small mammals and ectoparasites in Scandinavia. - In: Biocontrol of rodents (Hansson, L. and Nilsson, B. eds.). Ecological bulletins/NFR 19, Stockholm. pp 73-98.
- Brummer-Korvenkontio, M. 1966. Tick ecology and virus isolations from ticks in Finland. - Proc. I Int. Congr. Parasitol. (Roma 21-26 Sep. 1964). Vol. 2.
- Černý, V. 1957. Die Saisondynamik der Zecke *Ixodes ricinus* auf den von Zecken befallenden Waldflächen. - Československa parasitologie 4: 57-86.
- Černý, V. 1959. Horizontalmigration bei der Zecke *Ixodes ricinus* L. - Zoologické listy 8: 208-212. (in Czech, German summary).

- Edler, A. 1972. Ectoparasitic mites (Acarina) from small mammals in southern Sweden. - Ent. Tidskr. 93: 100-112.
- Edler, A. 1973. Seasonal changes and host relationships of mites on small mammals in southern Sweden. - Folia parasitol. (Praha) 20: 75-87.
- Edler, A. and Nilsson, A. 1973. Numerical relations between groups of ectoparasites infesting small mammals. - Ent. scand. 4: 274-282.
- Edwards, E.E. and Arthur, D.R. 1947. The seasonal activity of the tick *Ixodes ricinus* L., in Wales. - Parasitology 38: 72-85.
- Hansson, L. 1967. Index line catches as a basis of population studies on small mammals. - Oikos 18: 261-276.
- Honzakova, E., Olejnicek, J., Černý, V., Daniel, M. and Dusabek, F. 1975. Relationship between number of eggs deposited and body weight of engorged *Ixodes ricinus* female. - Folia parasitol. (Praha) 22: 37-43.
- Johnsen, P. 1946. Bidrag til Kundskaben om den danske Ixodidae Fauna. - Ent. Meddr. 24: 397-401.
- Lees, A.D. and Milne, A. 1951. The seasonal diurnal activities of individual sheep ticks (*Ixodes ricinus* L.). - Parasitology 41: 189-208.
- Loew, J., Radda, A., Pretzmann, G. and Groll, E. 1963. Untersuchungen in einem Naturherd der Frühsommer-Meningoencephalitis (FSME) in Niederösterreich. - Zentralbl. Bakt. Parasitenk. Infektionskr., Hyg. 190: 183-206.
- Macleod, J. 1939. The seasonal and annual incidence of the sheep tick, *Ixodes ricinus*, in Britain. - Bull. ent. Res. 30: 103-118.
- Mehl, R. 1972 a. Ektoparasitter på grevling i Norge. - Fauna 25: 265-274.
- Mehl, R. 1972 b. Lopper, flått og midd på piggsvin i Norge. - Fauna 25: 186-196.
- Mehl, R. 1972 c. Ektoparasitter på rødrev i Norge. - Fauna 25: 247-257.
- Mermod, C., Aeschlimann, A. et Graf, J.-F. 1973. Écologie et éthologie d'*Ixodes ricinus* Linné 1758, en Suisse (Acarina, Ixodoidea). Première note: Fluctuation numérique. - Acarologia 15: 197-205.

- Mermod, C., Aeschlimann, A. et Graf, J.-F. 1973. Écologie et éthologie d'*Ixodes ricinus* L. en Suisse. Deuxième note: Comparaison des population 1972 et 1973. - *Acarologia* 16: 612-620.
- Milne, A. 1945. The ecology of the sheep tick, *Ixodes ricinus* L. The seasonal activity in Britain with particular reference to northern England. - *Parasitology* 36: 142-152.
- Nilsson, A. 1974. Distribution, host relations and seasonal occurrence of *Ixodes trianguliceps* Birula (Acarina) in Fennoscandia. - *Folia parasitol. (Praha)* 21: 233-241.
- Pretzmann, G., Radda, A. und Loew, J. 1964. Studien zur Ökologie von *Ixodes ricinus* L. in einem Endemiegebiet der Frühsommermeningoencephalitis (FSME) im Bezirk Neunkirchen (Niederösterreich). - *Z. Morph. Ökol. Tiere* 54: 393-413.
- Saikku, P. and Brummer-Korvenkontio, M. 1975. Tick-borne viruses in Finland. - *Medical Biology* 53: 317-320.
- Saikku, Ulmanen, I. and Brummer-Korvenkontio, M. 1971. Ticks (Ixodidae) on migratory birds in Finland. - *Acta Ent. Fenn.* 28: 46-51.
- Schulze, P. 1929. Erster Beitrag zur Zeckenfauna Dänemarks. - *S.B. naturf. Ges. Rostock.* 3: 120-123.
- Schulze, P. 1930. Erster Beitrag zu einer Zeckenfauna Schwedens. - *Medd. Göt. Mus. Zool. Avd.* 54. 18 pp.
- Tambs-Lyche, H. 1943. *Ixodes ricinus* og piroplasmosen i Norge. - *Norsk Vit. Tidskr.* 9-12: 337-542.
- Traavik, T. and Mehl, R. 1975. Tick-borne viruses in Norway. - *Medical Biology* 53: 321-324.
- Öhman, C. 1961. The geographical and topographical distribution of *Ixodes ricinus* in Finland. - *Acta Soc. pro Fauna et Flora Fenn.* 74: 1-38.

	Larvae	Nymphs	Adults	Total
Kullaberg	7955	4276	224	12455
	63.8 %	34.3 %	1.8 %	
Övedskloster	303	614	10	927
	32.7 %	66.2 %	1.1 %	

Tab. 1. Distribution of developmental stages of I. ricinus obtained by the blanket method at Kullaberg and Övedskloster.

Stampen

	n	$\bar{x}$	SE	t	P	% infested	χ^2	P
Jan	22	-				-		
Feb	10	-				-		
Mar	35	-				-		
Apr	52	1.27	0.46	0.50	NS	30.8	1.50	NS
May	17	1.94	1.07	0.25	NS	47.1	12.69	***
Jun	35	21.51	8.78	0.25	NS	91.4	18.29	***
Jul	19	1.79	0.91	0.26	NS	36.8	0.07	NS
Aug	36	3.67	0.64	3.67	***	33.3	23.38	***
Sep	36	6.33	0.96	5.91	***	88.9	32.82	***
Oct	92	0.74	0.16	24.24	***	32.6	14.94	***
Nov	88	0.09	0.03	75.06	***	8.0	1.96	NS
Dec	20	-				-		

Tab. 2. Monthly infestation pattern of I. ricinus larvae on small mammals at Stampen and Kullaberg. ***= $P < 0.001$, **= $0.01 > P > 0.001$, *= $0.05 > P > 0.01$, NS = not statistically significant.

Kullaberg

	n	$\bar{x}$	SE	t	P	% infested	χ^2	P
Jan	65	0.03	0.02	11.09	***	3.1	0.22	NS
Feb	41	0.05	0.03	1.02	NS	4.9	0.31	NS
Mar	6	-		3.94	***	-	6.49	*
Apr	49	4.65	1.09	0.67	NS	55.1	5.03	*
May	37	9.70	2.53	0.60	NS	78.4	5.72	*
Jun	47	2.81	1.45	0.27	NS	53.2	4.55	*
Jul	34	4.50	2.05	0.44	NS	29.4	10.54	**
Aug	47	3.89	0.07	0.62	NS	66.0	8.54	**
Sep	19	28.05	6.23	0.38	NS	100.0	2.31	NS
Okt	63	11.90	1.84	2.69	**	88.9	21.50	***
Nov	73	2.18	0.49	8.28	***	52.1	20.40	***
Dec	58	0.22	0.09			13.8		

Tab. 2. cont.

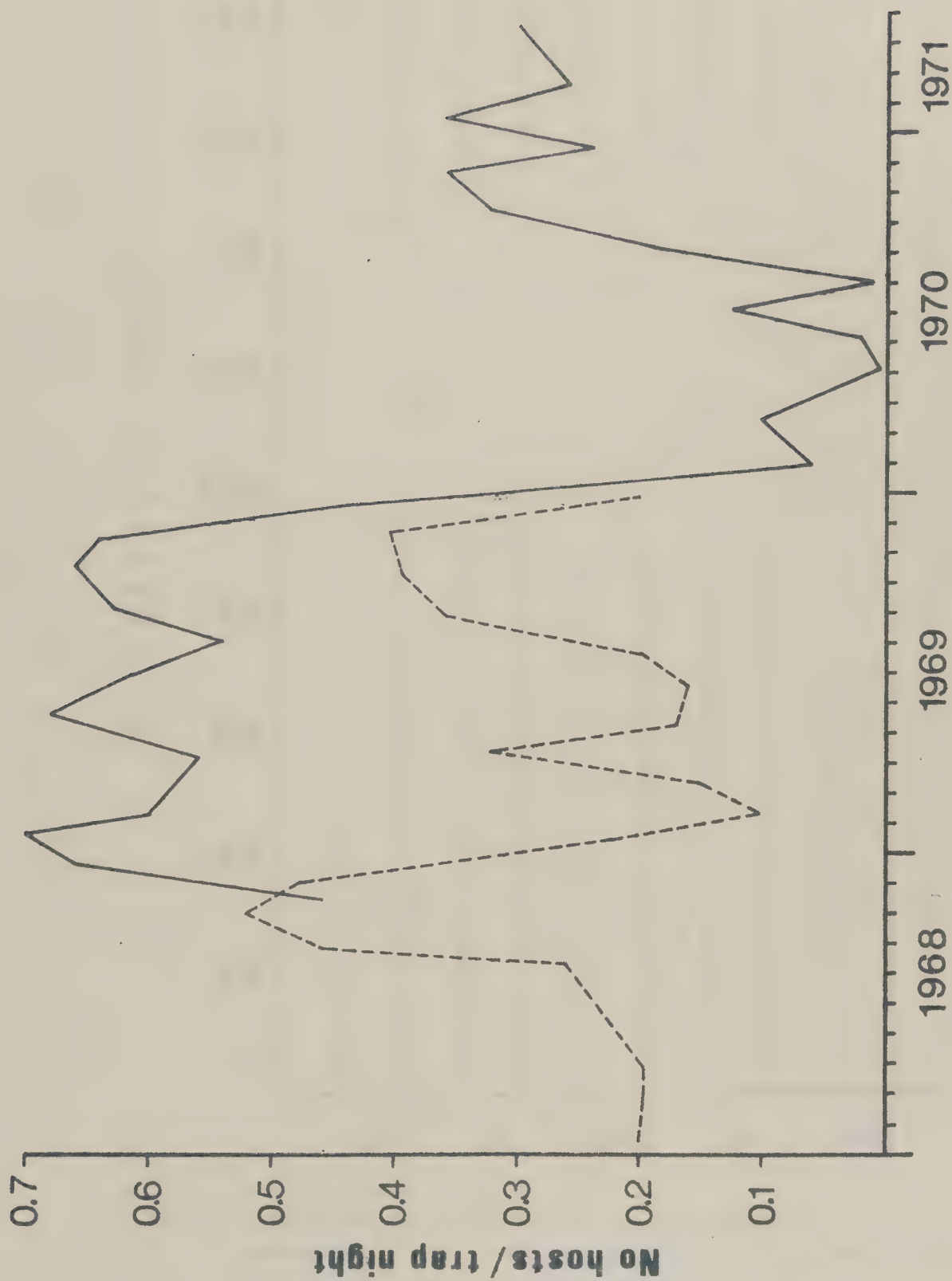
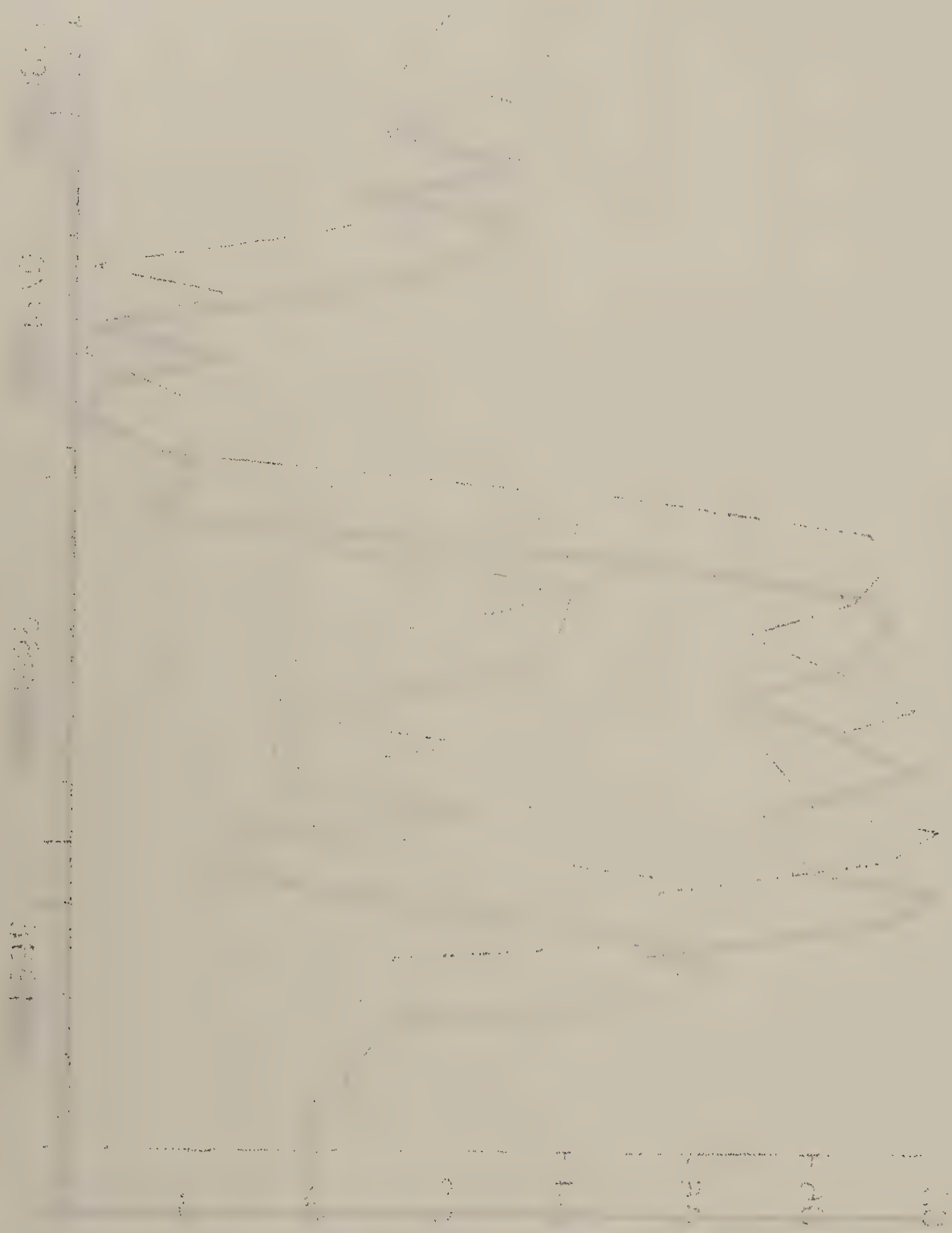


Fig. 1. Population fluctuations in small mammals at A. Stampen and B. Kullaberg.



1000 1500 2000 2500 3000

1 2 3 4 5 6 7

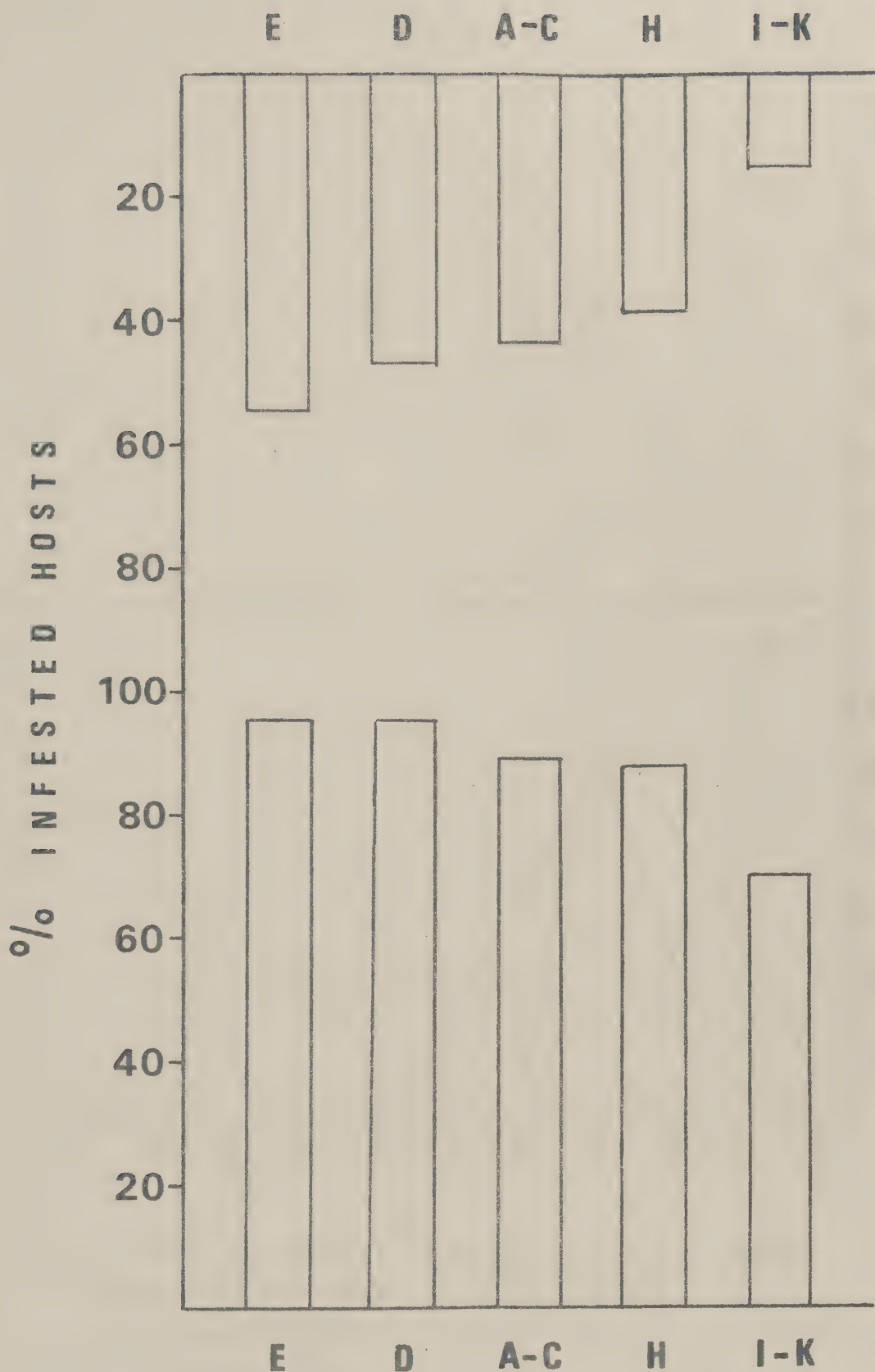


Fig.2. Infestation frequencies of Ixodes ricinus on small mammals in different habitats at Kullaberg. A,B. Oak forest. C.Windpressed oak forest close to the sea. D.Alder forest. E,F.Pine forests. G.Juniper. H.Eco-
tone. I-K.Grasslands.

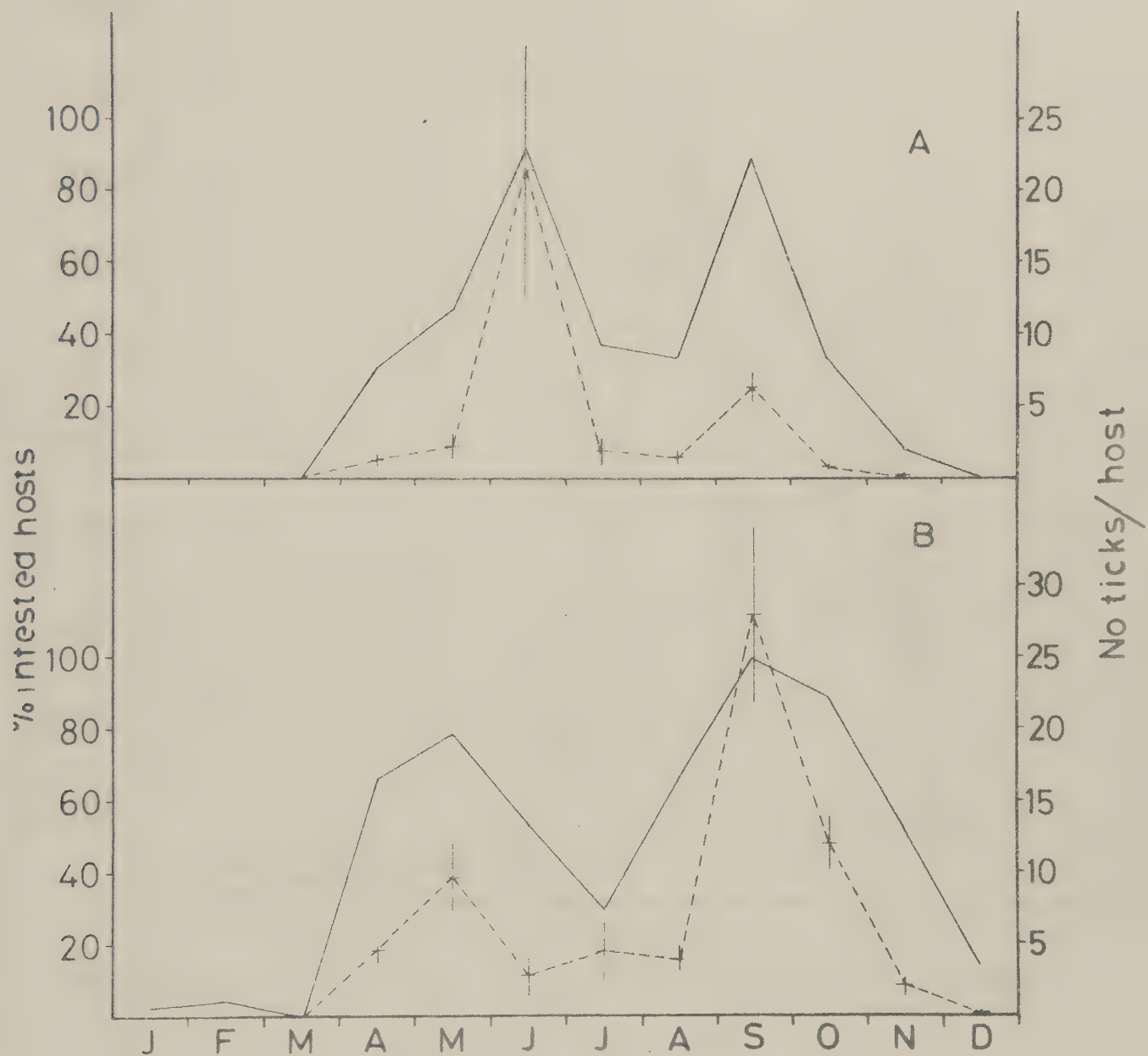


Fig.3. Seasonal occurrence of *Ixodes ricinus* on small mammals at A.Stampen and B.Kullaberg.

———— infestation frequency;----- number of ticks per host. Vertical bars indicate SE.

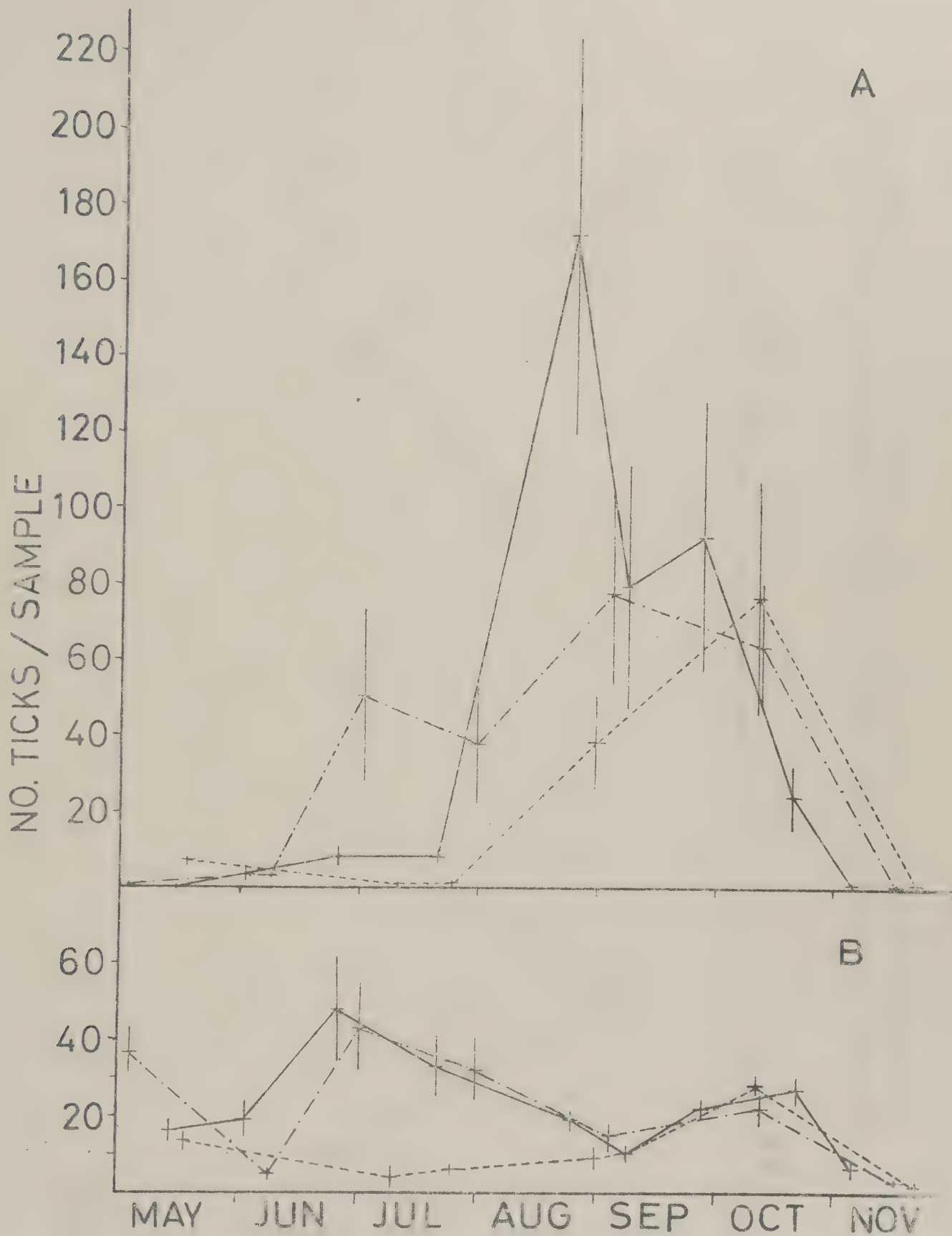


Fig.4. Seasonal occurrence of *Ixodes ricinus* in vegetation (blanket method) at Kullaberg. A. larvae and B. nymphs. — 1968, - - - 1969, - · - · - 1970. Vertical bars indicate SE.

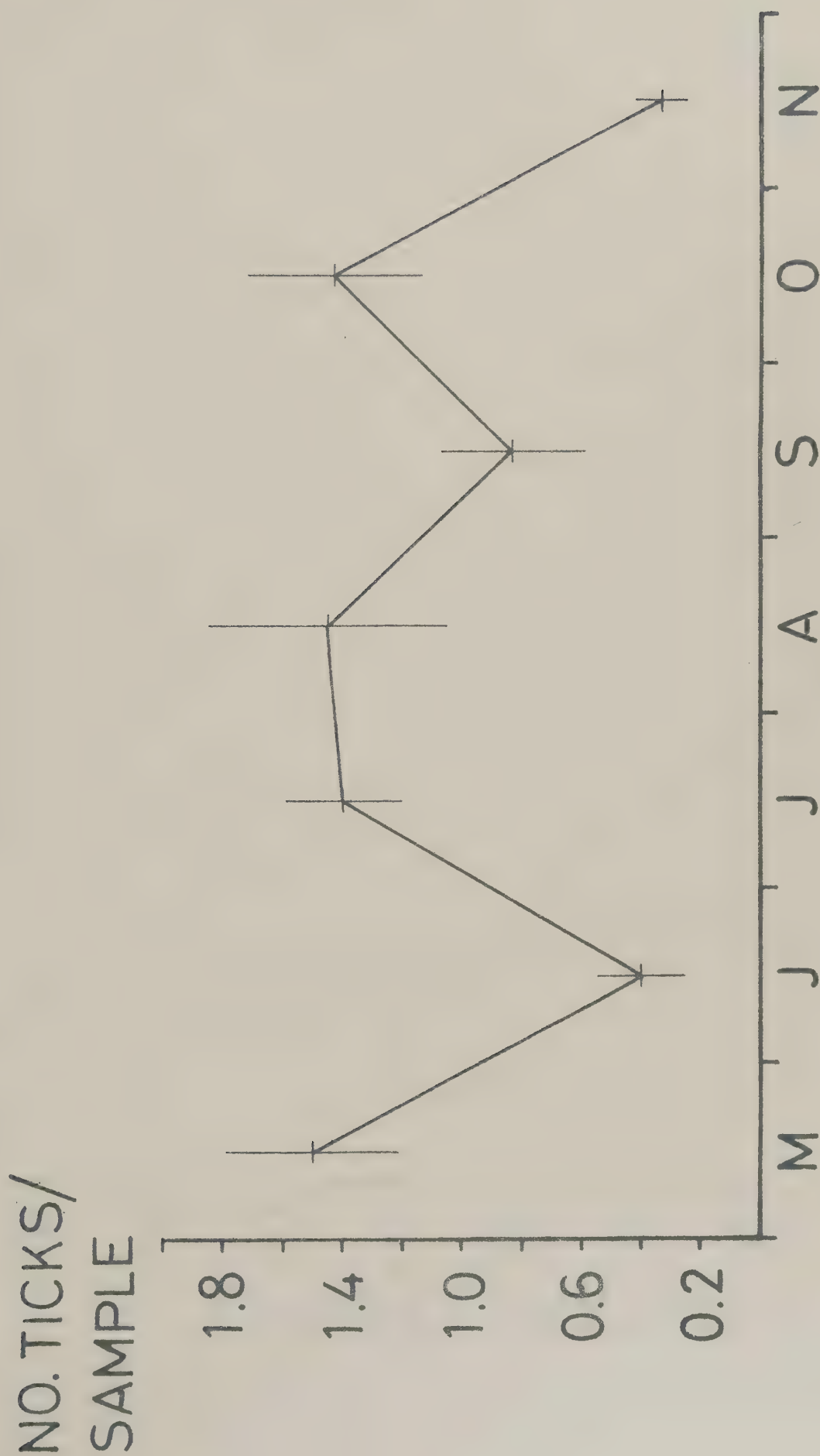


Fig.5. Seasonal occurrence of adult *Ixodes ricinus* in vegetation (blanket method) at Kullaberg. Pooled data from 1968 - 1970. Vertical bars indicate SE.

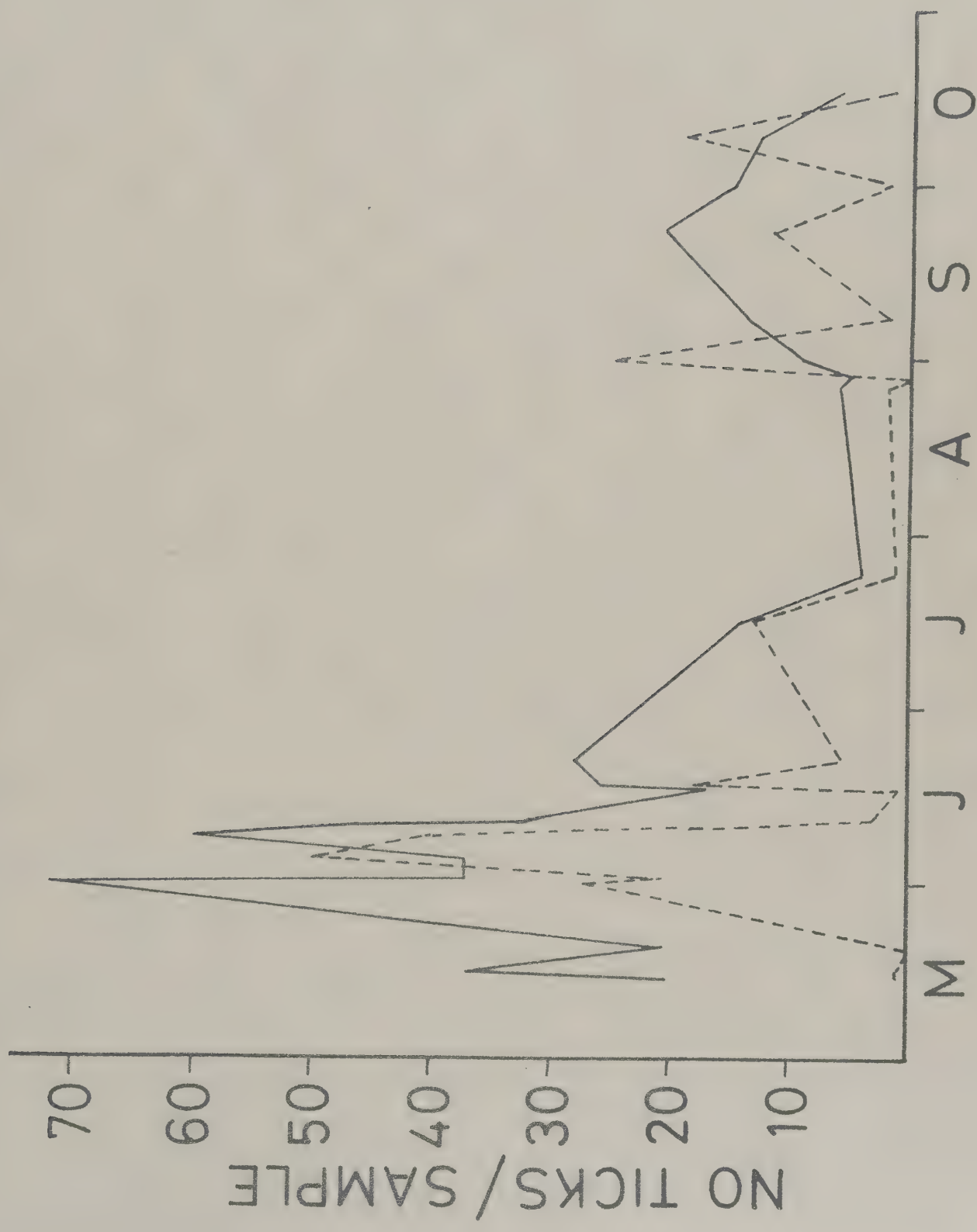


Fig.6. Seasonal occurrence of Ixodes ricinus at Övedskloster.----- larvae, ----- nymphs

Parasitism of female *Ixodes trianguliceps* by the males

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Nilsson, A. 1975. Parasitism of female *Ixodes trianguliceps* by the males. – *Oikos* 26: 295–298.

Two male *Ixodes trianguliceps* Birula were found feeding on females of the same species. Males leave distinct scars on the females following detachment. 27.8% of 162 studied females had been attacked by males in this way. The number of scars increased with increasing degree of engorgement. In partially fed females the scar frequency was 41%. Attachment was more numerous near the female genital opening, suggesting that males normally feed in connection with copulation. The high scar frequency on fed females suggests that copulation normally occurs on the small mammal host.

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Было обнаружено, что два самца *Ixodes trianguliceps* Birula питались на самках того же вида. Самцы оставили на теле самок заметные рубцы после своего ухода. 27,8% из 162 исследованных самок стали таким образом жертвами самцов. Количество рубцов увеличивалось с повышением степени насыщенности кровью. У частично высосанных самок частота встречаемости рубцов составляла 41%. Повреждения наиболее многочисленны около генитального отверстия самок, что свидетельствует о том, что самцы обычно питаются во время копуляции. Высокая частота повреждений на теле самок показывает, что копуляция обычно происходит на мелких млекопитающих.

The feeding of male ixodid ticks differs from that of the females, nymphs and larvae. In species living in the vegetation, like *Ixodes ricinus* L. and *I. persulcatus* Schulze, the males seem to be facultative blood feeders, being able to fertilize without having a blood meal (Balashov 1968). In these species males are often found on the host. In some ixodid species living in host burrows such as *I. lividus* (Koch), *I. hexagonus* Leach, *I. canisuga* Johnston and *I. trianguliceps* Birula, males are rare on the hosts and are thought not to feed (Arthur 1962). Copulation possibly takes place inside burrows off the host.

In this study about 15000 small mammals were examined for adult *I. trianguliceps*. 147 mammals yielded 162 female ticks and 19 males. The material was collected throughout Sweden, Norway, Finland and Denmark (Nilsson 1974 a).

Material (preserved in 80% ethanol) for scanning electron microscopy was dehydrated through a series of ethanols and toluols, cleaned by ultra sonic treatment (Shear and Levi 1970), coated in vacuum, and examined with a Cambridge Stereoscan MK II A microscope.

Of the 19 males found on hosts, two were firmly attached to the ventral surface of the females (Fig. 1). The chelicerae and the hypostome had penetrated the body wall of the female and were completely embedded (Fig. 2). The position of the males was similar to that during copulation, but at a slightly oblique angle to the mid-ventral line.

Sectioning attached males and females revealed that the mouthparts of the male had penetrated through to



Fig. 2. Male *I. trianguliceps* with mouthparts penetrating female *I. trianguliceps* in the region of the genital opening (enlarged portion of Fig. 1). 140 $\times$.

the blood-filled gut. Eight non-attached males found on rodents were sectioned. In all of them blood residues were identified in the gut.

The penetration of the male mouthparts through the female body wall leave easily recognizable scars. They appear as small, distinct depressions (Figs 3, 4). 5% of the scars were found on the dorsal surface, but were



Fig. 1. Male *I. trianguliceps* with mouthparts penetrating female *I. trianguliceps* in the region of the genital opening. 45 $\times$.

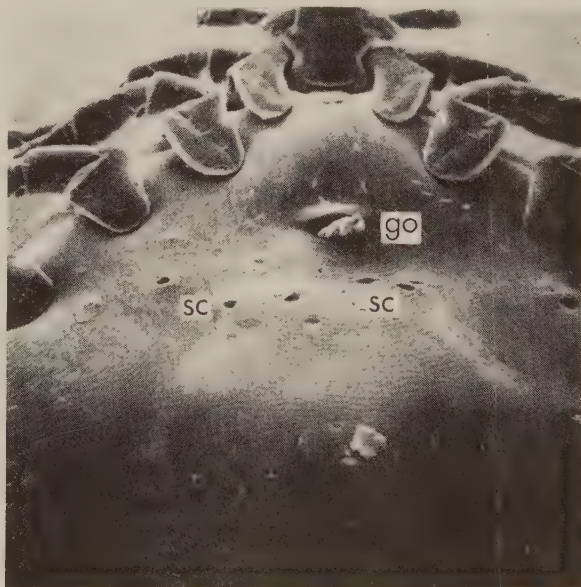


Fig. 3. Ventral surface of female *I. trianguliceps* showing scars caused by mouthparts of male *I. trianguliceps*. 45 $\times$. go = genital opening, sc = scars.

most numerous anteroventrally. 75% of the scars were near to and posterior to the genital opening (Fig. 5).

45 of the examined females (27.8%) had been attacked in this way and showed at least one scar. All females with scars had ingested a certain amount of blood. Of the partly engorged females 41.0% had scars. The mean number of scars per female was 0.7 and per fed female 2.4. No scars were found on males or nymphs.

When comparing females with different degree of engorgment with regard to the number of scars per female it was found that the number of scars increased with increasing engorgment (Fig. 6). Unfed females lacked scars.

Multiple scarring was common. 11 (24%) of the scarred females had three or more scars; the maximum being 17 found on an almost completely engorged female (Fig. 3).

17 males were found on hosts, which also carried females and only on one such host had a female not been attacked.

Blood loss by male feeding would appear detrimental to the female and her egg production, and in this respect the evolution of intraspecific parasitism is unusual. However, such male feeding does occur among ixodids. Nuttall and Warburton (1908) reported a male *I. trianguliceps* with its mouthparts penetrating a female, but thought it to be a misplaced attempt at copulation. In *I. holocyclus* Neumann, male feeding on the female seems to be common (Moorhouse 1966) and in *Hyalomma detritum* Schulze hungry males may feed on females (Usakov 1961). However, as long as the males feed on females which stay on a host, the females may compensate their blood loss by ingesting more from the host.

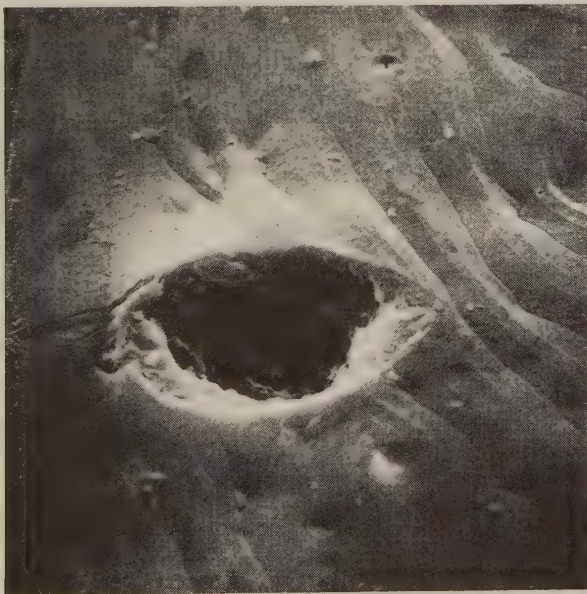


Fig. 4. Scar on ventral surface of female *I. trianguliceps* caused by mouthparts of male *I. trianguliceps*. 690 $\times$.

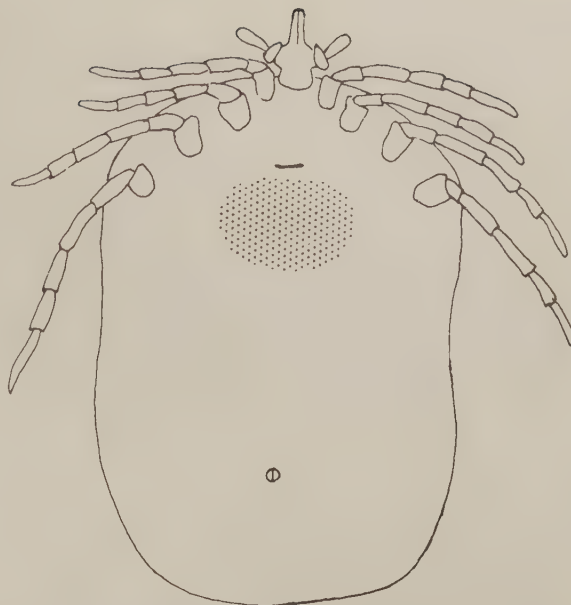


Fig. 5. Ventral surface of female *I. trianguliceps*. 75% of scars were found within the shaded area.

The fact that male *I. trianguliceps* are rarely found on small mammal hosts – in this study they comprise about 11% of all the adult *I. trianguliceps* – has resulted in the opinion that they do not feed and that copulation takes place off the host. Moreover the mouthparts of the male are considered ill-adapted for feeding on small mammals or for copulation on the host (Arthur 1962). Assuming that there are as many males as females in an *I. trianguliceps* population, and that males stay on the hosts only during mating and feeding, males must remain on the hosts for about 12 h to have the same chance of being recorded as the females. As copulation lasts for only 2 h (Arthur 1962), a period of about 12 h on the host may be sufficient for the male to mate and feed. This may explain the rare records of male *I. trianguliceps* on hosts (Nilsson 1974 a, b).

mean No.
scars

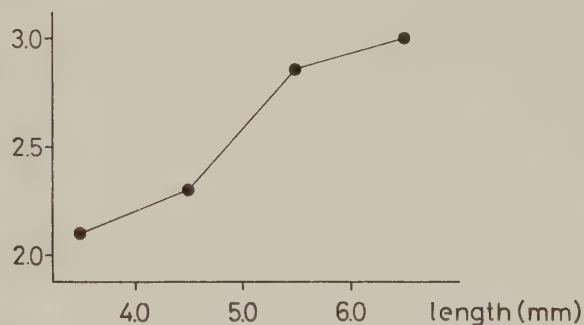


Fig. 6. Mean number of scars on female *I. trianguliceps* attacked by males in relation to body length of the female.

In this study the records of feeding male *I. trianguliceps* do not demonstrate if feeding is obligate, or facultative as in *I. ricinus*. The high frequency of females with scars indicates however, that males normally feed in this way, as in *I. holocyclus* (Moorhouse 1966).

Since the majority of scars were found near the genital opening, feeding seems to be associated with mating, although this can not be ascertained from the present material. In *I. holocyclus*, where the distribution and position of scars on females are similar to those of *I. trianguliceps*, male feeding seems to precede copulation (Moorhouse 1966). It should be noted that in my material there were two females which lacked scars but had spermatophores attached to the genital opening.

The high frequency of scars on females that were partially fed suggests that even a higher proportion of fully engorged females are attacked before falling off the host. The frequency may be higher than 41%, so it may be assumed that copulation normally occurs on the small mammal host, though mating off the host in burrows cannot be excluded.

As in *I. holocyclus* (Moorhouse 1966) there was an increasing number of scars per female with increasing degree of engorgement. There seems to be a selection against copulation with unfed females; perhaps female attractants may operate (cf. Berger et al. 1971). It is more likely, however, that it is a function of time: more engorged females have been exposed for a longer period and have a greater chance of being attacked by males than newly infested unfed females.

Acknowledgements

I thank Prof. P. Brinck for advice and criticism, Mrs U. Holmberg for translating the paper by Usakov, Mr R. Odselius for the sectioning, and Dr H. Myhrberg for operating the scanning electron microscope. The work was financed by the Nordic Council for Terrestrial Ecology, the Royal Physiographic Society in Lund, the Research Institute of National Defence, and the Faculty of Mathematics and Natural Sciences of the University of Lund.

References

- ARTHUR, D. R. 1962. Ticks and disease. — Pergamon Press, London.
- BALASHOV, YU. S. 1968. Bloodsucking ticks (Ixodoidea) — vectors of diseases of man and animals. — Nauka Publishers, Leningrad. (In Russian). Transl. 500, Medical Zoology Department, United States Naval Medical Research Unit No. 3, Hoogstraal, H. and Tatchell, R. J. (Ed.), Cairo, Egypt, 1972.
- BERGER, R. S., DUKES, J. C. and CHOW, Y. S. 1971. Demonstration of a sex pheromone in three species of hard ticks. — J. Med. Ent. 8: 84–86.
- MOORHOUSE, D. E. 1966. Observations on copulation in *Ixodes holocyclus* Neumann and the feeding of the male. — J. Med. Ent. 3: 168–171.
- NILSSON, A. 1974a. Distribution, host relations, and seasonal occurrence of *Ixodes trianguliceps* Birula (Acari) in Fennoscandia. — Folia parasitol. 21: 233–241.
- 1974b. Host relations and population changes of *Ixodes trianguliceps* (Acari) in northern Scandinavia. — Oikos 25: 315–320.
- NUTTALL, G. H. F. and WARBURTON, C. 1908. Ticks: A monograph of the Ixodoidea. Pt II: Ixodidae. — University Press, Cambridge, pp. 195–348.
- SHEAR, W. A. and LEVI, H. W. 1970. Cleaning museum specimens of spiders and myriapods with ultrasonics. — Bull. British Arachn. Soc. 1: 117.
- USAKOV, U. Y. 1961. Homovampirism in ixodid ticks. — Zool. Zhur. 40: 608. (In Russian with English summary).

Spatial differentiation of ectoparasites on small mammals

by Anders Nilsson

Abstract

Different ectoparasitic species occur on different areas of the small mammal host: chiggers in the ear muzzle, ticks on the ears and other parts of the head, fleas and lice on the back and most gamasid mites on the posterior part of the host body.

The distribution might be affected by 1) the mechanical interference of the host. Thus attached species such as ticks and chiggers occur in areas where direct predation is limited and small and/or very mobile species are found on other parts of the body. 2) Interaction between parasitic species. In areas where species meet, there might be a segregation in time or in space. Species such as Laelaps agilis (C.L. Koch) and Haemogamasus nidi Michael are most frequently found within a restricted area on the host, but differ in their seasonal occurrence. In other combinations of species, such as in fleas and lice, there are marked differentiations in body areas used. These differentiations may be evolutionary fixed or manifested at first when species meet. 3) Abundance, where an increasing abundance enlarge the habitat used.

1. Introduction

The distribution pattern of ectoparasites on their hosts is a result of an interaction between the parasites and the hosts and the co-existence among the parasites.

The ectoparasites dealt with in this paper are ticks, chiggers, gamasid mites, fleas and lice. Lice and certain gamasid mites are permanent parasites while fleas and certain mite species are "nest-dwellers", which use the host for feeding and/or copulation. Among the last mentioned species, oviposition, development and moulting may occur in the nest. Others, such as Ixodes ricinus and Neotrombicula spp. develop in the vegetation, but feed on the host once in each developmental stage.

How do the ectoparasites disperse and distribute on their host species? In order to study the dispersal and the spatial distribution of the ectoparasites on the hosts, a number of small mammals were collected. At the same time, the structure of the ectoparasitic community and possible interferences between species were analysed.

The distribution of ectoparasites on their hosts has been examined in a number of species (Nelson et al. 1975) but there are few quantitative studies at the community level.

2. Material and methods

About 500 small mammals from southern Scandinavia were investigated to determine the prediliction places of the ectoparasites. Four host species dominated the material: Apodemus flavicollis Melch., A. sylvaticus L., Clethrionomys glareolus (Schreb.) and Sorex araneus L. A few Microtus agrestis L. were included.

Hosts were trapped in live traps and put into polythene bags with diethyl ether, which killed them and the ectoparasites. Most bodies were frozen before examination in the laboratory. In cases where it took some time to get them to the laboratory the bodies were preserved in a mixture of equal amounts of 80 % ethyl alcohol and 4 % formic aldehyde. This fluid was also injected into the peritoneal cavity of the host animal.

Ectoparasites were removed with tweezers in the laboratory and preserved in 80 % ethanol before identification.

The body of the hosts was divided into ten areas (Fig. 1) and the location of each ectoparasite was noted.

The extent of the different areas varies between species and even between different age-groups of the same species. This has not been taken into account below.

A minor bias may appear in the material preserved in ethanol because some of the ectoparasites were washed off the host into the preservation fluid. This affected lice, fleas and gamasid mites in a few cases. Ticks and mostly also chiggers are securely anchored into the host skin and were not affected.

More than 4500 ectoparasites were collected.

3. Results

3.1. Preferred sites on the host species

Frequent ectoparasites (species or groups of species) on a selection of host species are presented in Tab. 1.

Ixodes ricinus and I. trianguliceps were the only tick species found on the small mammal hosts. In this paper, only the larvae of I. ricinus are dealt with. They are referred to as I. ricinus. Nymphs and adults prefer larger hosts and are rarely found on small mammals. I. ricinus has a pronounced preference for the head (areas 1 and 2), ranging from 65.5 % on Sorex araneus to 89.6 % on Apodemus sylvaticus. The G-test of independence (Sokal and Rohlf 1973) showed that differences in the distribution of I. ricinus on the various host species were highly significant ($P < 0.001$).

Other preferred sites of I. ricinus on rodents are distal (and thin haired) parts of the body, such as the tail and feet: more than 80 % of the ticks in area 3, were found on the front feet. The occurrence of ticks on the tail and feet was especially marked in Apodemus spp. Almost all I. ricinus collected from the belly and back of the rodents occurred at wounds. Such wounds are especially frequent in reproductive males and might be caused by fighting with other males.

On S. araneus the distribution of the ticks differed markedly. Thus the back (areas 3 and 4) contained 30.3 % of the I. ricinus. Less than 2 % were attached to the feet.

Within the preferred areas (1 and 2) on the rodents, I. ricinus were attached mainly at the base of the whiskers and to the lower jaw, and in a narrow strip near to the ear margin. The most distal parts - lips, nose and ear margins - were rarely infested.

I. trianguliceps is confined to tunnel-inhabiting small mammals and consequently all developmental stages are found on these hosts (Ulmanen 1972, Nilsson 1974a, 1974b, Randolph 1975). Altogether 93 specimens were found: 78 larvae, 14 nymphs and 1 female. I. trianguliceps was even more concentrated in area 2 than I. ricinus. Only 4 specimens were found away from the ears; one female in area 3 and two nymphs in area 1 (Tab. 2).

The distribution of the parasitic Acari is described in Tab. 2. Some species occurred in low numbers and are not dealt with.

The chiggers found were all Neotrombicula zachvatkini and were confined to the ears. 93 % were found on C. glareolus and the rest on A. flavicollis.

Laelaps agilis is a permanent parasite of Apodemus spp. and is seldom found on other host species (Edler 1969). It prefers areas 5 and 6 where they concentrate in a narrow strip between the fur and the more sparsely haired feet and tail. Areas 4 and 9 are close to areas 5 and 6, which may explain the rather high frequency there.

There was a significant difference in the distribution of L. agilis on the two Apodemus species. On A. flavicollis the legs were the most preferred site. On A. sylvaticus most specimens were found in area 6 ($P < 0.001$).

On M. agrestis, L. hilaris showed a strong preference for the tail base (area 6) and Hyperlaelaps microti for the hind legs (area 5). Together they had a similar distribution to that of L. agilis on Apodemus.

Eulaelaps stabularis and Haemogamasus nidi are nest parasites which usually occur together on the same host species.

On Apodemus they are often found together with L. agilis. Most H. nidi were found in area 6, while E. stabularis aggregated in area 4, a few mm in front of area 6.

Apart from the tick species and the trombiculids, the well represented species of Acari showed a preference for the posterior part of the host animals.

There was no significant difference in the overall distribution of fleas on the host species investigated ($P > 0.05$).

A few species made up the main part of the fleas: Ctenophthalmus agyrtes (Heller) dominated on Apodemus spp. and C. glareolus and Palaeopsylla soricis (Dale) on S. araneus. The spatial differentiation of the flea species was analysed in specimens of A. sylvaticus and C. glareolus from southernmost Sweden (Fig. 2). On A. sylvaticus, C. agyrtes dominated and was found primarily in area 3. Typhloceras poppei Wagn. was found in about equal amounts on the head and in area 3. Nosopsyllus fasciatus Bosc. showed strong preference for the posterior part of the host, while Rhadinopsylla pentacantha (Roths.) was found on the head (only three specimens).

On C. glareolus there was a tendency to the same spatial distribution, C. agyrtes and Megabothris turbidus (Roths.) preferring the anterior part of the back and C. uncinatus (Wagn.) the posterior part.

A similar spatial differentiation was found in the two species of Anoplura on C. glareolus. Hoplopleura acanthopus (Burm.) constituted 55.8 % of the lice on C. glareolus and was most frequent on the anterior part of the body. The other species, Polyplax spinulosa (Burm.) (44.2 %), was found primarily in area 4 (Tab. 1). On the Apodemus species, however, where only 4 specimens of H. acanthopus were found, P. spinulosa clearly preferred area 3.

3.2. Preferred sites on hosts of different age and sex

Hosts were divided into the following groups (Myllymäki 1970): Adult (reproductive) males, adult females, subadults in at least their second pelage but with immature gonads, and juve-

niles still bearing remains of their first pelage. Postreproductive hosts (with regressed gonads) were not found during the trapping periods.

S. araneus is excluded, because there were mainly adult males in the material.

The I. ricinus distribution on adult male A. flavicollis (Tab. 3) differed significantly ($P < 0.001$) from other age and sex groups. Significant differences ($0.001 < P < 0.01$) were also found for adult females compared with juveniles. Other combinations did not differ significantly.

On A. sylvaticus most combinations differed significantly from each other. The significance was $P < 0.001$ for juveniles and each of the other groups, and $0.001 < P < 0.01$ for adult males compared with adult females and adult females compared with subadults.

Finally males and females of C. glareolus differed ($P = 0.05$).

Areas 1 and 2 had a similar parasite load: only juveniles. A. sylvaticus differed significantly from subadults and females. The above differences were therefore primarily caused by the distribution in areas other than the head region.

Significant differences were found in the distribution of L. agilis on A. flavicollis (Tab. 4). However, the distribution did not differ significantly between adult males and females or between subadults and juveniles. Between preadults (subadults + juveniles) and adults (adult males + adult females) the difference was highly significant ($P < 0.001$). No such differences were found for A. sylvaticus.

3.3. Effects of crowding

The relative distribution of the ectoparasites may change when their density changes. (Fig. 3, Tab. 5).

At low overall abundances of I. ricinus, the ears (area 2) of rodents were strongly preferred. When abundance increased there was a relative decrease in ear infestation and an increase on the rest of the head (area 1). This applies to Apo-

demus spp. and C. glareolus, while S. araneus differed. At low ectoparasite abundance, area 1 had most I. ricinus. With increasing density the head infestation decreased relatively, while the number of ticks on the ears and back increased.

At low densities of L. agilis on A. flavicollis the ectoparasites were evenly distributed between the most preferred sites - areas 5 and 6. With increasing abundance the frequency of mites increased in areas 5 and 10 with a simultaneous decrease in infestation of area 6.

4. Discussion

Host deparasitation behaviour probably plays an important role for controlling the abundance (e.g. Bell and Clifford 1964) and distribution of ectoparasites on their hosts. It seems likely that the evolutionary response to mechanical interference by the host results in a division of body areas of the host between species or groups of parasite species. Thus attached (immobile) species such as ticks and chiggers are primarily found on the head, where they are unreachable for direct predation by the host. This distribution is unlikely to be a result of their elimination from other areas of the host. As was found in I. ricinus, there is a directed movement towards the predilection places (Nilsson in ms). The possibilities for the host to eliminate ticks or chiggers on the head by scratching must be regarded as limited, especially for chiggers inside the ear muzzle, but also for the ticks on the flexible ears.

Species inhabiting areas which can be reached by the host are all small and/or very mobile, viz. fleas, lice and gamasid mites.

Kucheruk et al. (1956) found that the distribution of the tick Dermacentor marginatus Sulzer differed considerably between host species and they related this to differences in the deticking ability of the host. In the hedgehog the ticks were found all over the body, but in A. sylvaticus, which was supposed to be an efficient groomer, the distribution was more concentrated. On the basis of the present results this would

mean that S. araneus is less efficient than A. sylvaticus and C. glareolus in eliminating I. ricinus. This is possible, but as mentioned above the distribution of I. ricinus larvae on the host body is probably mainly a result of tick behaviour.

For species mating on the host, and especially for those occurring at low densities, a small predilection area must be advantageous. For example, in I. trianguliceps, where adults are comparatively rare on the hosts (Ulmanen 1972, Nilsson 1974a, b, 1975, Randolph 1975), the chances of a male finding a female should increase considerably if searching is limited to a small area during the few days the female is present on the host.

In other cases separation between species in time or in space is manifested at first when they meet. From the present material it is not always clear whether interspecific competition is present or not. In some cases, however, the indications are strong.

The two tick species occupied partly the same areas of the host. In general the distribution pattern found in previous studies (e.g. Bauch 1972, Immler 1973 and Randolph 1975) agrees with the present results. There are differences, which may be caused by differences in infestation intensity. Although the presence or absence of interspecific competition was not examined in the present study because of the constant low density of I. trianguliceps, the large collections of ticks (and other ectoparasites; from various parts of Scandinavia; see Brinck-Lindroth et al. 1975) reveal that in areas where I. ricinus is very abundant, the density of I. trianguliceps is fairly low, whereas in areas where I. ricinus is less abundant, I. trianguliceps is more frequent. So far no locality has been found where there is a high abundance of both I. ricinus and I. trianguliceps. It is also to be noted that there is some separation between the tick species as regards the peaks of activity. The peak of activity for I. trianguliceps in spring (Nilsson 1974a) is earlier than that for I. ricinus (Nilsson in ms).

In the Apodemus species, three mite species occurred close to each other on the hosts. L. agilis, H. nidi and E. stabula-

ris prefer areas on the posterior part of the host. L. agilis and H. nidi were frequent in area 6 and E. stabularis in area 4, near area 6. A large material of mites from A. sylvaticus collected in Iceland gave the same results (Nilsson in prep.). Edler (1973) found that the seasonal occurrence of L. agilis differed between two South Swedish localities; H. nidi was most frequent in both localities, when infestation of L. agilis was low and vice versa. This suggests that there is a competitive interaction between these species, as between the two tick species occupying area 2.

L. hilaris and H. microti (both on Microtus) and L. agilis (on Apodemus) occupied the same areas on their hosts. In C. glareolus and S. araneus the corresponding areas were utilized to the same extent. However, L. clethrionomydis (Lange) occurring on C. glareolus in Central Europe and northern Scandinavia (Edler and Mrčiak 1975) and Hirstionyssus soricis (Turk) on Sorex may be ecological equivalents.

Among fleas there was also a spatial differentiation between the species on the host. The present results agree with findings in Iceland (in litt.), where A. sylvaticus is the only field-living small mammal (Bengtsson et al. 1976). It is infested by two flea species only: C. agyrtes and N. fasciatus. In parts of Iceland both flea species occur together while in other parts only N. fasciatus is present. The distribution of these two species on the host is not, however, affected by the presence or absence of the other species.

The two anopluran species were both frequent on C. glareolus, but were separated from each other with only a small overlap. This separation seems to be due to interspecific competition, which is supported by the fact that P. spinulosa, occurring on the posterior part of C. glareolus, is found on the anterior part of the host (Apodemus) where H. acanthopus is rare.

References

- Bauch, R.J. 1973. Zur Bionomie von Ixodes ricinus. III. Die Rolle der freilebenden Kleisäuger als Larvenwirte im DDR-Bezirk Magdeburg. - Angew. Parasitol. 14: 208-213.
- Bell, J.F. and Clifford, C. 1964. Effects of limb disability on lousiness in mice. II. Intersex grooming relationships. - Exp. Parasitol. 15: 340-349.
- Bengtson, S.-A., Nilsson, A., Nordström, S. and Rundgren, S. 1976. Body weights of Apodemus sylvaticus in Iceland. - Acta theriol. 21: 389-399.
- Brinck-Lindroth, G., Edler, A., Lundqvist, L. and Nilsson, A. 1975. Small mammals and ectoparasites in Scandinavia. - In: Biocontrol of rodents (Hansson, L. and Nilsson, B. eds.). Ecological Bulletins/NFR 19: 73-98. Stockholm.
- Edler, A. 1969. Ectoparasitic mites (Acarina) from small mammals in Central Sweden. - Ent. Tidskr. 90: 272-284.
- Edler, A. 1973. Seasonal changes and host relationships of mites on small mammals in southern Sweden. - Folia parasitol. (Praha) 20: 75-87.
- Edler, A. and Mrciak, M. 1975. Gamasina mites (Acari: Parasitiformes) on small mammals in northernmost Fennoscandia. - Ent. Tidskr. 96: 167-177.
- Immler, R.M. 1973. Untersuchungen zur Biologie und Ökologie der Zecke Dermacentor reticulatus (Fabricius, 1794) (Ixodidae) in einem Endemischen Vorkommensgebiet. - Mitt. Schweiz. Ent. Ges. 46: 1-70.
- Kucheruk, V.V., Nefedova, I.N. and Dunaeva, T.N. 1956. On the importance of the small mammals self-defence against the larvae and nymphs of the ixodid ticks. - Zool. Zh. 35: 1723-1727.
- Myllymäki, A. 1970. Population ecology and its application to the control of the field vole, Microtus agrestis (L.). - EPPO Publ. Ser. A 58: 27-48.
- Nelson, W.A., Keirans, J.E., Bell, J.F. and Clifford, C.M. 1975. Host-ectoparasite relationships. - J. Med. Ent. 12: 143-166.

- Nilsson, A. 1974 a. Distribution, host relations, and seasonal occurrence of Ixodes trianguliceps Birula (Acari) in Fennoscandia. - Folia parasitol. (Praha) 21: 233-241.
- Nilsson, A. 1974 b. Host relations and population changes of Ixodes trianguliceps (Acari) in northern Scandinavia. - Oikos 25: 315-320.
- Nilsson, A. 1975. Parasitism of female Ixodes trianguliceps by the males. - Oikos 26: 295-298.
- Randolph, S.E. 1975. Patterns of distribution of the tick Ixodes trianguliceps Birula on its hosts. - J. Anim. Ecol. 44: 451-474.
- Sokal, R.S. and Rohlf, F.J. 1973. Introduction to biostatistics. - Freeman, San Francisco.
- Ulmanen, I. 1972. Distribution and ecology of Ixodes trianguliceps Birula (Acarina, Ixodoidea) in Finland. - Ann. Zool. Fenn. 9: 111-115.

A. flavicollis

Species/Area	1	2	3	4	5	6	7	8	9	10	Total No.
I. ricinus	32.0	46.6	7.7	0.2	7.0		4.6	1.6	0.3		1351
L. agilis	2.7	0.9	7.7	8.1	43.7	18.5	2.7	2.3	2.3	11.3	222
Siphonaptera	3.3		64.8	17.2	3.3			9.0	1.6	0.8	122
P. spinulosa			65.4	7.8	3.8				3.8	19.2	26

A. sylvaticus

I. ricinus	40.0	48.0	4.4	0.8	2.7	0.2	2.9	1.0	0.1		1125
L. agilis			1.0	7.3	39.6	49.0			2.1	1.0	96
Siphonaptera	2.0		61.2	20.4	3.9			6.8	5.8		103
P. spinulosa	11.6	2.3	58.1	14.0	9.3		2.3		2.3		43

C. glareolus

I. ricinus	30.6	59.3	5.8	0.5	0.8		1.0	0.2	1.8		617
Trombiculidae		100.0									224
Siphonaptera	9.9		57.2	17.8	2.0	3.9		5.9	3.3		152
H. acanthopus	9.9		84.7	3.6	1.8						111
P. spinulosa			19.3	78.4	1.1		1.1				88

S. araneus

I. ricinus	34.9	30.6	20.2	10.1	0.8		0.8	1.6	1.2		258
I. trianguliceps	2.9	97.1									68
Siphonaptera	5.9		65.5	18.7	2.5		0.5	18.7	7.9	0.5	203

Tab. 1. Frequency of frequent species or groups of ectoparasites on the body areas of a selection of small mammal species.

Statistical tests (Tab. 1. cont.)

L. ricinus

	G	df	
A. flavicollis - A. sylvaticus	62.39	8	$P < 0.001$
A. flavicollis - C. glareolus	100.84	7	$P < 0.001$
A. flavicollis - S. araneus	154.52	7	$P < 0.001$
A. sylvaticus - C. glareolus	60.90	8	$P < 0.001$
A. sylvaticus - S. araneus	140.80	8	$P < 0.001$
C. glareolus - S. araneus	118.94	7	$P < 0.001$

L. agilis

A. flavicollis - A. sylvaticus	48.80	9	$P < 0.001$
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Siphonaptera

A. flavicollis - A. sylvaticus	4.02	5	NS
A. flavicollis - C. glareolus	14.38	6	$0.01 < P < 0.05$
A. flavicollis - S. araneus	2.84	5	NS
A. sylvaticus - C. glareolus	15.19	6	$0.01 < P < 0.05$
A. sylvaticus - S. araneus	7.76	5	NS
C. glareolus - S. araneus	14.33	6	$0.01 < P < 0.05$

P. spinulosa

A. flavicollis - A. sylvaticus	20.73	7	$0.001 < P < 0.01$
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		1	2	3	4	5	6	7	8	9	10	Total No.	Number infested hosts				
													A.f	A.s	C.g	M.a	S.a
<i>Ixodes ricinus</i> L.	F	1188	1645	250	40	138	2	105	37	19		3424	57	83	60	1	20
<i>I. trianguliceps</i> Birula	X	3	89	1								93	1	8	2	2	10
<i>Neotrombicula zachvatkini</i> (Schluger)	F		242									242	3	8	19		
<i>Laelaps agilis</i> (C.L. Koch)	P	6	2	18	25	135	88	6	7	5	26	318	44	41	2		
<i>L. hilaris</i> (C.L. Koch)	P			1		3	28			2	2	36					12
<i>Hyperlaelaps microti</i> (Ewing)	P	3	1	2	5	36	5			1	2	55					10
<i>Eulaelaps stabularis</i> (C.L. Koch)	N	5	1	5	11	5	1	1		4	1	34	1	12			
<i>Haemogamasus nidi</i> Michael	N	2		3	3	4	12			1	9	34	8	11	6	2	

Tab. 2. Distribution of ticks, chiggers and parasitic mites on the bodies of hosts. F = field-living species, N = nest inhabitants, P = permanent parasites, X = *I. trianguliceps* is not a nest inhabitant but mostly occurs in tunnels (see Randolph 1975)

Area	1	2	3	4	5	6	7	8	9	10	Total No.
<u>A. flavicollis</u>											
♂ ad	37.1	50.6	3.6	0.2	3.6		2.1	2.5	0.3		
♀ ad	30.3	46.0	3.5	0.5	8.3		5.8	0.2	0.5		
subad	25.5	34.9	17.0		13.2		9.4				
juv	21.8	41.3	14.5		12.3		7.8	2.2			
Total No.	432	630	104	3	95		62	21	4		1351
<u>A. sylvaticus</u>											
♂ ad	40.9	48.3	5.2	1.3	0.9	0.4	2.7		0.2		
♀ ad	40.6	49.0	3.5		4.6		2.3				
subad	48.7	41.1	3.3	1.9	0.6		3.2	0.6			
juv	28.8	51.4	4.5		5.1		4.5	5.6			
Total No.	450	540	49	9	30	2	33	11	1		1125
<u>C. glareolus</u>											
♂ ad	31.1	58.2	6.1	0.7	0.2		0.7	0.2	2.7		
♀ ad	31.3	63.3	3.6		1.2		0.6				
subad	16.0	68.0	8.0		4.0		4.0				
juv	35.3	35.3	17.6		5.9		5.9				
Total No.	189	366	36	3	5		6	1	11		617

Tab. 3. Frequency of Ixodes ricinus on the body areas of different sex and age groups in three rodent species.

Statistical tests (Tab. 3. cont.)

		G	df	
<u>A. flavicollis</u>	♂ ad - ♀ ad	47.02	7	$P < 0.001$
	♂ ad - subad	59.28	7	$P < 0.001$
	♂ ad - juv	64.22	7	$P < 0.001$
	♀ ad - subad	7.10	7	NS
	subad - juv	5.33	5	NS
<u>A. sylvaticus</u>	♂ ad - ♀ ad	22.83	7	$0.001 < P < 0.01$
	♂ ad - subad	8.35	8	NS
	♂ ad - juv	47.20	8	$P < 0.001$
	♀ ad - subad	19.47	6	$0.001 < P < 0.01$
	♀ ad - juv	28.50	5	$P < 0.001$
	subad - juv	29.65	6	$P < 0.001$
<u>C. glareolus</u>	♂ ad - ♀ ad	14.07	7	$P = 0.05$
	♂ ad - subad	9.01	7	NS
	♂ ad - juv	39.50	7	$P < 0.001$
	♀ ad - subad	5.32	4	NS
	♀ ad - juv	9.90	4	$0.01 < P < 0.05$
	subad - juv	4.56	4	NS

	1	2	3	4	5	6	7	8	9	10	Total No.
♂ ad	6.1	1.5	13.6	7.6	39.4	22.7	3.0	3.0		3.0	66
♀ ad	2.0		14.0	10.0	44.0	18.0	2.0	4.0		6.0	50
subad		3.5		6.9	51.7	17.2				20.7	29
juv	1.3		1.3	7.8	44.2	15.6	3.9	1.3	6.5	18.2	77
All	2.7	0.9	7.7	8.1	43.7	18.5	2.7	2.3	2.3	11.3	222

Tab. 4. Frequency of L. agilis on the body areas of different sex and age groups of A. flavicollis.

<u>Statistical tests</u>		G	df	
<u>A. flavicollis</u>	♂ ad - ♀ ad	3.74	8	NS
	♂ ad - subad	20.41	8	$0.001 < P < 0.01$
	♂ ad - juv	43.46	8	$P < 0.001$
	♀ ad - subad	11.61	5	$0.01 < P < 0.05$
	♀ ad - juv	18.43	8	$0.01 < P < 0.05$
	subad - juv	5.49	5	NS

No. of parasites host ⁻¹	1	2	3	4	5	6	7	8	9	10	Total No.
1 - 5		3.7	9.3	9.3	31.5	31.5	1.9	3.7	1.9	7.4	54
6 - 10	7.7		12.3	9.2	32.3	18.5	3.1	1.5	4.6	10.8	65
> 10			3.9	8.7	54.4	11.7	2.9	1.0	1.0	16.5	103

Tab. 5. Frequency of Laelaps agilis on the body areas of Apodemus flavicollis in relation to the infestation intensity.

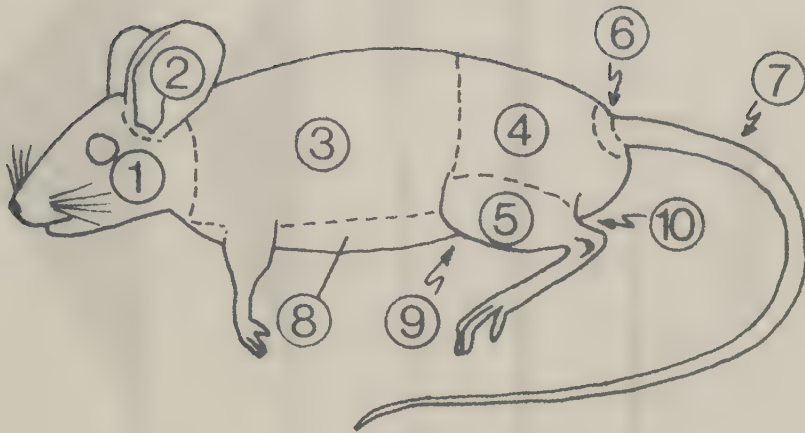


Fig. 1. Division of a small mammal host into ten arbitrary areas, useful for describing the distribution of ectoparasites.

1. Head, except the ears.
2. Ears.
3. Anterior part of back, including neck and front legs. The area comprises about 2/3 of the back.
4. Posterior part of back, excluding area 6.
5. Hind legs.
6. Tail base - a 3 mm broad strip.
7. Tail
8. Antero-ventral part below area 3.
9. Postero-ventral part below area 4.
10. Groin.

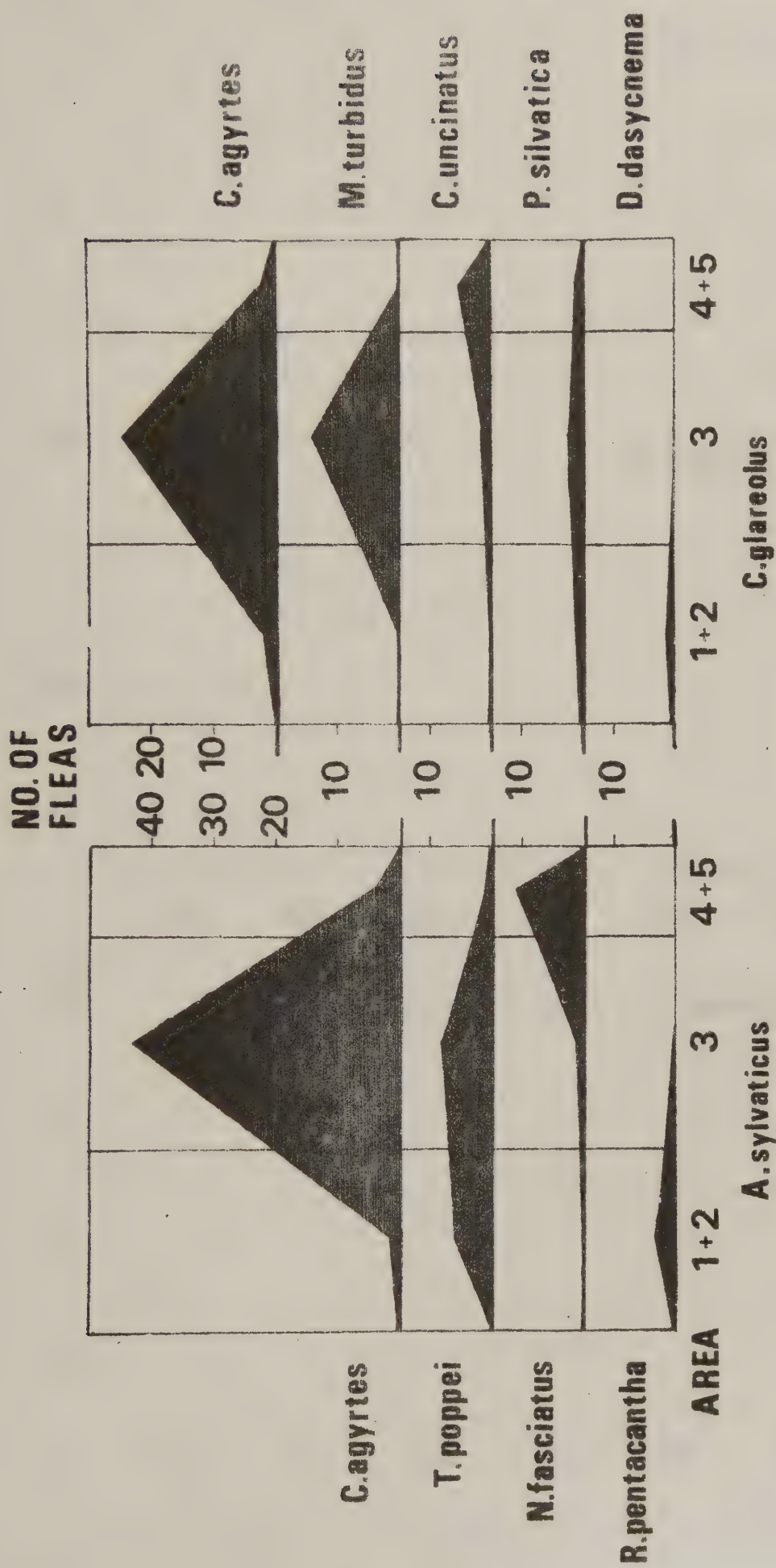
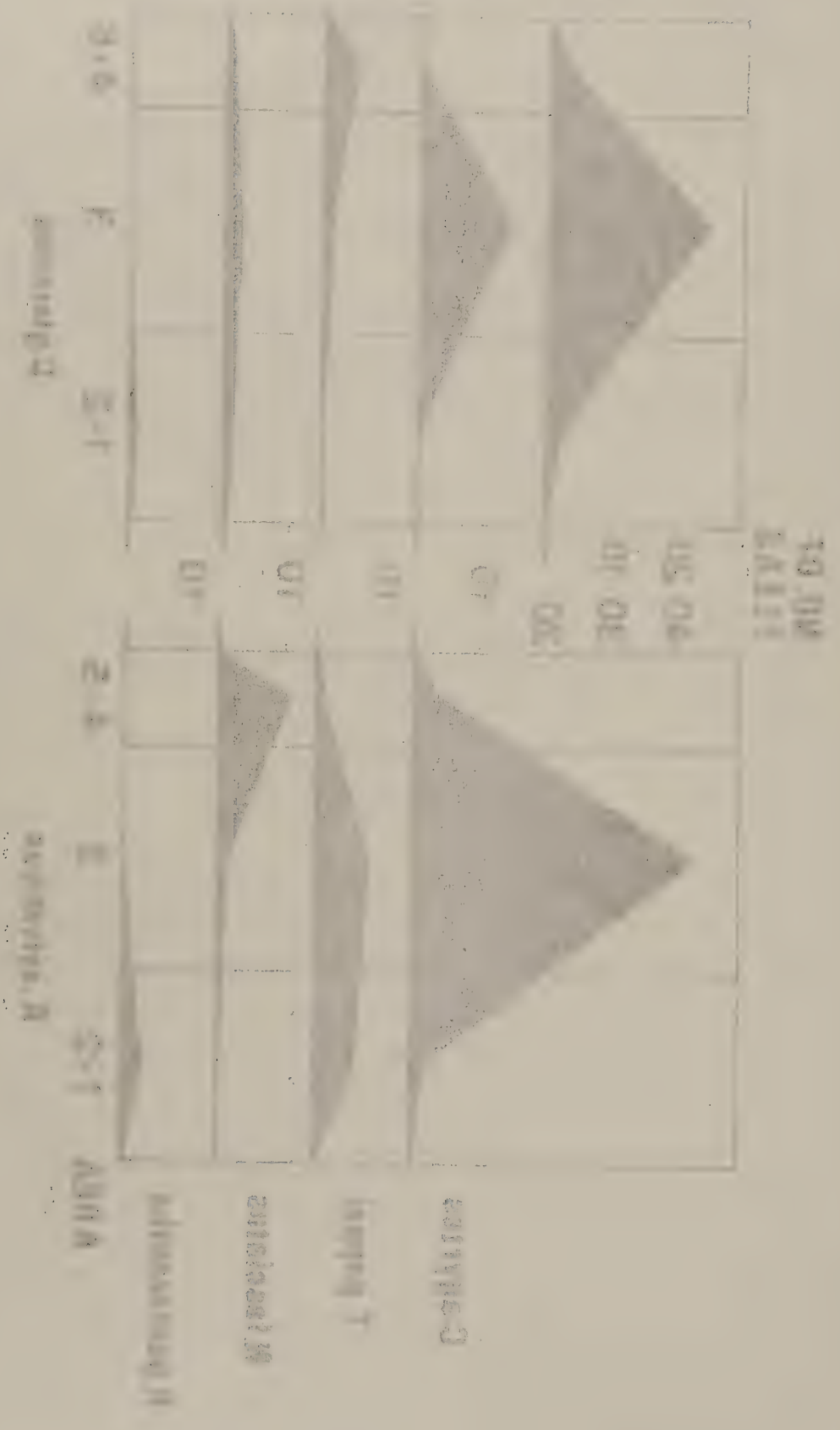


Fig.2. Distribution of fleas on the head and back (areas 1-5) of *Apodemus sylvaticus* and *Clethrionomys glareolus* from southernmost Sweden.



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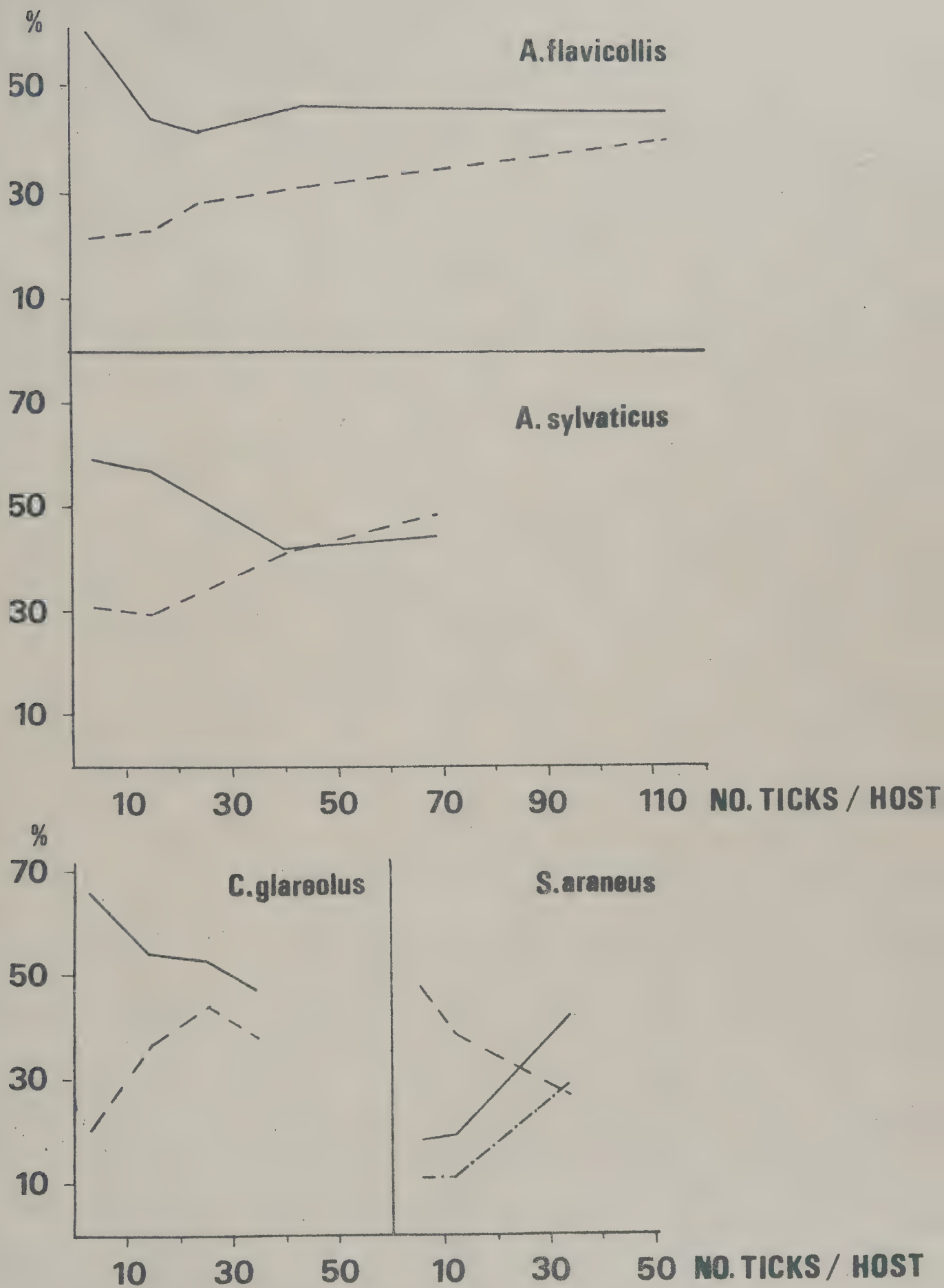
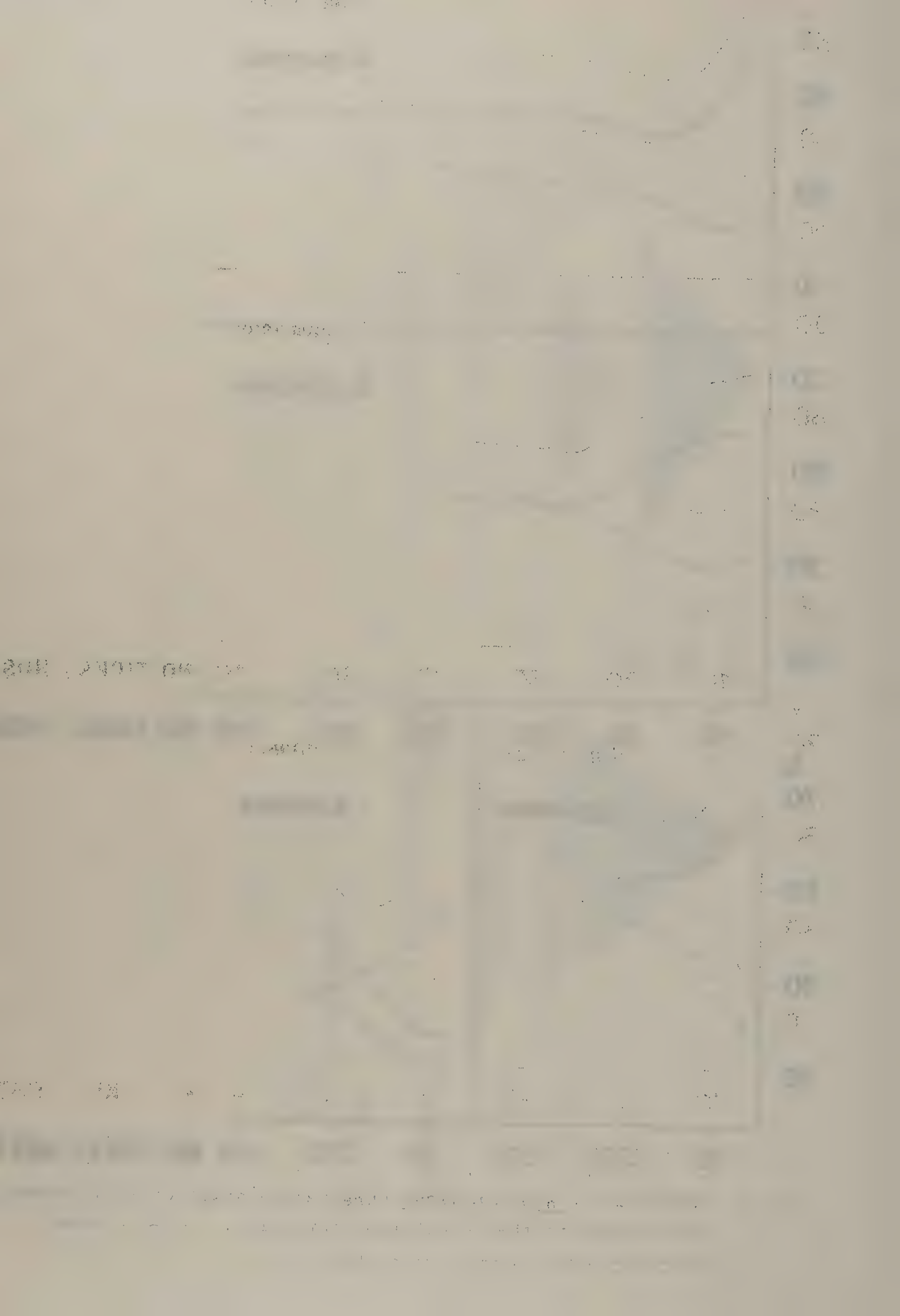


Fig.3. Frequency of *Ixodes ricinus* on the body areas of small mammals in relation to the infestation intensity. ----- area 1, ————— area 2, — · — · — area 3.



Host selection and movements of Ixodes ricinus (Acari) larvae on small mammals

by Anders Nilsson and Lars Lundqvist.

Abstract

The clumped distribution of Ixodes ricinus L. larvae in the vegetation causes a highly overdispersed distribution on small mammal hosts. This distribution pattern fits with the negative binomial distribution.

Apodemus sylvaticus L. has shorter daily active time and range and hence probably picks up fewer ticks from the vegetation. In spite of this A. sylvaticus carries considerably more ticks than Clethrionomys glareolus Schreb. and Sorex araneus L. in the field.

In laboratory experiments, this difference between rodents was even more pronounced. The reason for such differences in infestation is that the ticks do not accept the various host species to the same extent. Thus, 8 % in C. glareolus and 53 % in A. sylvaticus of introduced larvae succeeded in engorging. In A. sylvaticus the engorged larvae had a higher mean weight than in C. glareolus.

In the fur a larger part of the ticks had more directed and faster movements towards their predilection places on the head on A. sylvaticus than on C. glareolus. In S. araneus only a few ticks moved at all. The majority stayed on the spot where they had been placed.

The behaviour of the ticks on the host body explains the differences in attachment sites found in the field on different host species.

1. Introduction

Ectoparasites, like other biota, may be specialists or generalists, i.e. they have a more or less restricted host selection. Ixodes ricinus L. is catholic in its host selection and is capable of infesting not only terrestrial birds and mammals but also lizards (Arthur 1963).

The developmental stages of this 3-host tick species, larva, nymph and adult, are, however, more or less confined to different groups of hosts. The adults and nymphs prefer larger hosts and are seldom found on small mammals, which in turn may be regarded as important hosts for the larvae.

The survival of an I. ricinus population is dependent on the high relative humidity in its microhabitat (Macleod 1934, 1935). In southern Sweden this condition is often found in successional stages of woods, with a dense bush and luxuriant field layer (Nilsson in ms), where there is also a supply of hosts.

In such areas Apodemus sylvaticus L., Clethrionomys glareolus Schreb. and Sorex araneus L. dominate the small mammal fauna, although each is infested by I. ricinus to different extents (cf. e.g. Mermod et al. 1973).

Our hypothesis is, that such differences in infestation of I. ricinus larvae on various small mammal host species are caused not only by differences in encountering the larvae in the vegetation, but also by differences in the acceptance of the various species as host.

2. Material and methods

2.1. Infestation pattern in the field

Host animals were collected in May and November 1964 - 68 at Kullaberg, southern Sweden. The I. ricinus larvae showed high activity in May and low activity in November (Nilsson in ms). The age and reproductive stage of the host population were fairly homogenous in spring and autumn. Overwintered adults dominated in May, while in November all were subadults, apart from

a few postreproductive animals. Host animals were live-trapped, placed in polythene bags, killed with diethyl ether, and then preserved in a mixture of equal amounts of 80 % ethyl alcohol and 4 % formic aldehyde (water solution). Ticks were removed with tweezers in the laboratory (Edler and Nilsson 1973).

Host infestation by I. ricinus was described in terms of the incidence (% infested hosts), arithmetic mean $\bar{x}$ (number of ectoparasites per total number of hosts) variance s^2 , and the ratio $s^2/\bar{x}$. These values were calculated separately for spring and autumn (Tab. 1). Material collected during two sampling periods was large enough to enable a detailed analysis as to infestation of different sexes and reproductive stages of the hosts (Tab. 2).

The negative binomial distribution (defined by $\bar{x}$ and the exponent k) has been used as a model for the distribution of several parasites (Bliss and Fischer 1953, Davids 1973, Randolph 1975). This model was applied to the distribution of I. ricinus larvae on small mammal species. To obtain a clear picture of the spring distribution, the observed and expected frequencies were pooled into classes (Fig. 1). In classes where the expected frequency value exceeds 5, a χ^2 -value was calculated, while the numbers of observed and expected ticks in the rest of the classes were pooled into one χ^2 -value (Bliss and Fischer 1953). Lists of FORTRAN - V program may be obtained from us.

2.2. Experimental infestation in the laboratory

Hungry I. ricinus larvae were placed on the middle of the back (zone 5 in Fig. 5) of specimens of A. sylvaticus and C. glareolus. Each host was then placed in a net cage (95 x 95 x 95 mm) with a supply of water and pellet food. The cage was kept on 15 mm high wooden blocks inside a polythene bowl. The inner rim of the bowl was provided with a thick layer of vaseline to prevent escape of emigrating ticks.

Before ticks were transferred, the hosts were anaesthetized intraperitoneally with 0.06 g enallynalmnatrium per 1000 g body weight (Brietal-Sodium[®]), which made handling of the ani-

mals easier. Host animals usually remained anaesthetized for about 10 minutes. They usually woke up within 2 - 3 minutes after the ticks had been introduced.

Ticks were especially watched for the first few hours after transference. Notes were made on emigrating ticks, the time for dropping of engorged ticks and their weight after engorgement. The period of feeding was determined as the mean between two consecutive observations, not exceeding 5 hours.

To avoid possible immunity reactions (Trager 1939, Riek 1962) all hosts were reared in the laboratory and used once. 54 adult C. glareolus and 28 adult A. sylvaticus were used for the experiments.

30 I. ricinus larvae were placed on each host. In some cases larvae collected in the field were used, but mostly they were reared in the laboratory. No differences were noticed between them as regards infestation success or weight after engorgement. As there was a possibility of differences in infestation success between different batches of laboratory-reared larvae, the experiments with C. glareolus and A. sylvaticus were run concurrently.

2.3. Behaviour after introduction

Hungry larvae were released on the back of the hosts; 50 mm from the nose tip of C. glareolus and A. sylvaticus and 40 mm in S. araneus. No differences were observed as regards the behaviour of the ticks on live (anaesthetized) and dead hosts. Experiments were therefore performed with dead animals at 21° C and 80 % R.H. Killed hosts were kept 2 - 4 hours under these conditions before use. All shrews, however, were trapped in the field and were kept deep frozen before use.

The distance the introduced ticks moved and their orientation in relation to the host were recorded for each specimen. Each observation lasted 16 minutes, although in some cases the distribution was also checked after 1 hour.

Altogether 272 larvae were studied: 100 on A. sylvaticus, 136 on C. glareolus and 36 on S. araneus. Apart from subadults

of S. araneus, only adult rodents were used. All hosts had healthy fur and were used once.

3. Results

3.1. Infestation pattern in the field

The incidence (% infested hosts) was similar in the three host species. The highest value was found for A. sylvaticus, followed by C. glareolus and then S. araneus. This situation pertained in spring as well as in autumn (Tab. 1).

The mean number of larvae per host was significantly greater on A. sylvaticus than on C. glareolus ($P < 0.001$). There was no significant difference between C. glareolus and S. araneus. In autumn when there was low tick activity, there were significant differences between subadults of the three species.

In A. sylvaticus both sexes were about equally infested (no significant difference). In C. glareolus the adult male had far more ticks than the adult female in spring ($P < 0.001$). In autumn, however, the difference was less pronounced, but still significant ($0.05 > P > 0.01$) (Tab. 2).

Variance was high in all three host species, although lower in C. glareolus in spring as well as in autumn. The ratio $s^2/\bar{x}$ was used as a measure of the degree of clumping (Randolph 1975). This ratio varies with the variance, and is higher in spring, especially for A. sylvaticus (Tabs 1 and 2).

The frequency distribution of larvae on the host species is given in Fig. 1, together with expected values of the negative binomial distribution. Generally, both k and $\bar{x}$ are higher in spring, and the distribution pattern differs considerably between high and low tick activity.

3.2. Experimental infestation in the laboratory

The feeding success of larvae differed significantly between host species ($P < 0.001$) (Tab. 3). In A. sylvaticus 53 % of the introduced ticks succeeded in engorging, but only 8 % in C. glareolus. The feeding period (71 hours), however, did not differ as regards host species.

Most ticks that did not establish themselves left the host within the first few hours (Fig. 2). In C. glareolus 30 %, 47 % and 83 % of the introduced ticks had emigrated after 0.5, 1 and 3 hours respectively. For A. sylvaticus corresponding values were 4 %, 14 % and 21 %.

Some ticks were not recovered: 6 % for C. glareolus and 23 % for A. sylvaticus (Fig. 2).

Fig. 3 shows that the mean weight of engorged ticks from C. glareolus differed significantly from those from A. sylvaticus ($t = 2.72$; $0.05 > P > 0.01$).

The relation between feeding period and mean weight of engorged larvae may differ between the host species (Fig. 4). In A. sylvaticus those larvae with short feeding periods were lighter than the others, but the values were not significant ($P < 0.05$). In C. glareolus, however, the differences were significant ($0.05 > P > 0.01$). Ticks infesting C. glareolus for 4 days or more, reached about the same weight as ticks infesting A. sylvaticus for the same time.

3.3. Behaviour of ticks after introduction

Movements of the ticks was restricted to the surface of the fur of the host. Therefore, orientation and movements of the ticks could easily be observed.

In Fig. 5 the recorded spatial distribution of the ticks on the different host species is related to time after introduction. The distribution data were grouped into class widths of 10 mm. The classes or zones were numbered from 1 to 9, where zone 1 is the most anterior part of the host and zone 9 the most posterior (the tail excluded). Zones 1 - 3 are equivalent to the head of the host, where zone 3 includes the ears.

3 - 4 minutes after introduction, 50 % of the ticks had moved more than 10 mm on C. glareolus as well as on A. sylvaticus. In A. sylvaticus movement was exclusively towards the head, while in C. glareolus many moved in other directions. After a few minutes ticks were recorded in all zones on C. glareolus, although most were anterior of the release point. After 16 minutes, 87 % of the ticks on A. sylvaticus and 68 % on C. gla-

reolus were found on the head (zones 1 - 3), where the speed decreased and an accumulation of the ticks occurred. On S. araneus most of the ticks did not leave the place of introduction during the experimental period, although the small movements that did occur in some specimens were directed forwards.

The rate of movement towards the predilection places on the head was measured in terms of the mean and median rates of movement of the ticks (Fig. 6). The mean rate of movement of ticks differed considerably between the host species, more so than it did for the median rates of movement. In A. sylvaticus tick with the median rate of movement reached zone 3 after 6 minutes and in C. glareolus after 7 minutes, while mean values were 6.5 minutes and 11.5 minutes, respectively. The rate of movement was highest during the first few minutes following introduction. The median rate of movement of ticks was calculated for the first 4 minutes following introduction. On A. sylvaticus this was approximately 4.5 mm min^{-1} and on C. glareolus 3.5 mm min^{-1} . Corresponding mean values were 1.5 mm min^{-1} and 0.9 mm min^{-1} , respectively. Some specimens had, however, a considerably greater rate of movement (Fig. 5).

The orientation of the ticks in relation to the host body was also recorded (Fig. 7). Immediately after introduction, most ticks turned their body against the prevailing hair direction of the host, i.e. towards the host's head. However, some hid in the fur. 85 % of ticks on A. sylvaticus and 82 % on C. glareolus had orientated towards the host's head within a minute following introduction, although 30 % and 13 % respectively, were hidden in the fur. Throughout the experiments this orientation was rather constant: 90 - 95 % of the ticks on A. sylvaticus and about 80 % on C. glareolus.

The part hidden in the fur differed between the two host species, but in both increased with time, except for the first 4 minutes. In A. sylvaticus this was due to ticks reaching the predilection places on the head. In C. glareolus, however, ticks also hid for short periods on the back of the host, which may partly explain the differences found between the two host species.

On the vole some ticks moved forwards with few stops; others moved a small distance, stopped, crept down between the hairs, reappeared and then moved forward; while the remainder moved about in various directions from the release point.

In order to compare the emigration of unengorged ticks from live and dead hosts, some of the dead hosts were left with ticks for one hour. Emigration from live and dead hosts after one hour was almost identical (Tab. 4). After 15 minutes the number of emigrating ticks from live hosts was about the same as that from dead hosts, that had not moved forward at that time.

4. Discussion

In the calculated distributions, the s^2 was considerably greater than $\bar{x}$, indicating a clumped distribution of larvae on different host categories in spring as well as in autumn - a pattern which can be described by the negative binomial distribution.

Non-random distributions may be caused by (cf. Crofton 1971, Randolph 1975):

- i. Distribution of larvae and hosts in the area.
- ii. Previous infestation may change the susceptibility (negatively or positively) of the host to further infestation (Trager 1939, Riek 1962, Roberts 1968).
- iii. Host characteristics, e.g. species, age, sex, reproductive stage, size, activity and social position.

However, the observed distribution also reflects actual invasion and successful infestation. Therefore other factors must be considered, such as the duration of the parasite on the host.

Distribution of the larvae in the field can be dealt with at two levels: the individual distribution, which is highly overdispersed (aggregated), and the distribution of these aggregates. Nymphs and adults utilize larger host species with wider home-ranges. Since the lateral displacement of the ticks is highly limited in the field (Lees and Milne 1951, Černý

1959), nymphs and adults moult or oviposit in places where they land after dropping from the host. The eggs from a female are laid in one pile (800 - 5000 eggs; $\bar{x} = 2500$, Honzakova et al. 1975). The movements of the larvae are more or less vertical and there is a tendency for the larvae to gather (Arthur 1962). Thus, concentrated clutches of larvae are distributed over the area fairly independently of the small mammals.

If a small mammal passes through such an aggregate, it is very likely to be infested, but as it is probable that only some of the ticks are active at any one moment (Lees and Milne 1951) the aggregate is not drained by such a passage. This "plus-or-minus" event is probably the most important feature of the incidence and can be related to the locomotory activity of the host.

The number of ticks climbing onto a host passing through a larval aggregate, is probably species independent. However, the number of ticks still remaining after 4 hours (Fig. 2) seems to be species dependent. It was shown that the average feeding period of established ticks is the same on A. sylvaticus as on C. glareolus (Tab. 3), although those on C. glareolus are much smaller. Thus, 16 out of 30 ticks (53 %) became fully engorged on A. sylvaticus but only 2.5 out of 30 (8 %) on C. glareolus (Fig. 2). An average feeding period of 71 hours for established larvae gives an average stay on the host for all introduced larvae of about (71×0.53) 37.6 hours and (71×0.08) 5.7 hours, respectively (i.e. 6.6 times longer on A. sylvaticus). If we state as a null-hypothesis, that the locomotory activity of C. glareolus and A. sylvaticus is the same (and hence the picking up of ticks is equal) the means of larvae per host should be proportional to the stay of larvae on the host, that is $\bar{x}$ should be 6 - 7 times greater on A. sylvaticus than on C. glareolus. In spring female A. sylvaticus have almost 6 times as many ticks as female C. glareolus. But in all other cases this ratio is smaller (1.5 - 2.6) (Tabs 1 and 2), indicating that C. glareolus picks up more larvae than does A. sylvaticus. Several factors may be important for the process of picking-up, such as the area of ground covered per

unit time by the host (host size and distance moved) (Mohr 1961, Randolph 1975), the synchronization of host and tick diel activity and possibly also the size of home-range of hosts (Mohr op. cit., Randolph op. cit.). For C. glareolus, a longer activity period on the ground surface is indicated in several studies (e.g. Ashby 1972) and larger size of daily ranges of this species has been demonstrated by Nikitina et al. (1977). The interpretation of the results, however, is often complicated by differences in short-term rhythms and light regimes (Miller 1955, Brown 1956, Kikkawa 1964). This is especially complicated in S. araneus (Crowcroft 1954).

The orientation and movements of I. ricinus on the host differed between species. On A. sylvaticus the ticks moved faster towards the head than on C. glareolus. Only a few ticks moved forward on S. araneus during the experimental period: a feature which is probably reflected in the less concentrated distribution found on this host species in the field (Nilsson in ms). But for rodents almost all ticks are found on the head (Bauch 1973, Immler 1973, Nilsson in ms). The present experiments show that the ticks move from the place of introduction on the rodent host to the areas where they settle. This movement is directed against the direction of the host's fur and results in an accumulation of ticks on the head. Directed and rapid movement of the ticks reduces the risk of their being scratched off by the host.

The prevailing direction of the host's fur seems primarily important for the orientation of the ticks, whereas width, length and stiffness of the hair may influence the rate of movement of the ticks and also account for the differences found on and between different host species (cf. Fig. 5).

Some ticks left the host without settling; substantially more so for C. glareolus than for A. sylvaticus. This was not due to deticking activity (scratching) by the host, because about equal numbers of ticks left from both live and dead hosts. It is thus possible that at any given moment only a limited part of the tick population is capable of settling on C. glareolus, while a larger part of the population has these

qualifications when introduced to A. sylvaticus.

6 % of the ticks introduced to C. glareolus and 23 % to A. sylvaticus were not recovered and were probably eaten by the host. Such a difference between host species was found in laboratory studies with I. persulcatus Schulze (Nikitina and Zhmaeva 1963, Nikitina and Aristova 1964).

Predation probably occurs primarily during the tick migration towards the predilection places, i.e. when the ticks are less protected against host deticking activity. However, this may be reduced by the tick by rapid movement of the tick and hiding in the fur immediately after introduction and when disturbed. The hiding response might also reduce the risk of their being brushed off by the vegetation.

According to Kucheruk et al. (1956) host species with restricted distribution of ticks on their host bodies should be more efficient at eliminating ticks, than host species with a less concentrated tick distribution, e.g. the hedgehog. Nevertheless these differences in distribution need not necessarily depend exclusively on the deticking ability of the host. They may be a result of different stimuli for the ticks to move to and settle in predilection places. Randolph (1975) working with I. trianguliceps Birula on small mammals in the field, found that the deticking factor was unimportant for the infestation levels on various host species.

The mean weight of early dropped engorged larvae was lower than the weight of larvae, which had fed for a longer time. This was especially marked in C. glareolus. Although some ticks might have been scratched off by the host before being fully engorged. We consider this factor as less important, however, as the observed mean feeding period was the same on both species. Furthermore all engorged ticks which had dropped from C. glareolus or A. sylvaticus were alive and none appeared to have been injured.

The lower infestation and lower mean weight of engorged ticks on C. glareolus together with the restricted spatial distribution on the host (Nilsson in ms) intimates a host restriction in the I. ricinus larvae. Some ticks do not find suit-

able feeding sites and leave their hosts (actively or passively); others may remain at inferior feeding sites, resulting in shorter feeding periods and lower mean body weights, while the others remain at their predilection places, which in the case of C. glareolus results in a larger part of the ticks on the ears.

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References

- Arthur, D.R. 1962. Ticks and disease. - Pergamon press, Oxford.
- Arthur, D.R. 1963. British ticks. - Butterworth, London.
- Ashby, K.R. 1972. Patterns of daily activity in mammals. - Mammal Rev. 1: 171 - 185.
- Bauch, R.J. 1973. Zur Bionomie von Ixodes ricinus III. Die Rolle der freilebenden Kleinsäuger als Larvenwirte im DDR-Bezirk Magdeburg. - Ang. Parasitol. 14: 208-213.
- Bliss, C.I. & Fischer, R.A. 1953. Fitting the negative binomial distribution to biological data. - Biometrics 9: 176-200.
- Brown, L.E. 1956. Field experiments on the activity of the small mammals Apodemus, Clethrionomys and Microtus. - Proc. Zool. Soc. Lond. 126: 549 - 564
- Černý, V. 1959. Horizontalmigration bei der Zecke Ixodes ricinus L. - Zool. listy 8: 208 - 212. (In Czech. German summary.
- Crowcroft, P. 1954. The daily cycle of activity in British shrews. - Proc. Zool. Soc. Lond. 123: 715 - 729.
- Crofton, H.D. 1971. A quantitative approach to parasitism. - Parasitology 62: 179 - 193.
- Davids, C. 1973. The water mite Hydrachna conjecta Koenike, 1895 (Acari, Hydrachnellae), bionomics and relation to species of Corixidae (Hemiptera). - Neth. J. Zool. 23: 363 - 429.
- Edler, A. & Nilsson, A. 1973. Numerical relations between groups of ectoparasites infesting small mammals. - Ent. scand. 4: 274 - 282.
- Honzakova, E., Olejnicek, J., Černý, V., Daniel, M. & Dusbabek, F. 1975. Relationship between number of eggs deposited and body weight of engorged Ixodes ricinus female. - Folia parasitol. 22: 37 - 43.
- Immler, R.M. 1973. Untersuchungen zur Biologie und Ökologie der Zecke Dermacentor reticulatus (Fabricius, 1794)(Ixodidae) in einem endemischen Vorkommensgebiet. - Mitt. Schw. Ent. Ges. 46: 1 - 70.

- Kikkawa, J. 1964. Movement, activity and distribution of the small rodents Clethrionomys glareolus and Apodemus sylvaticus in woodland. - J. Anim. Ecol. 33: 259 - 299.
- Kucheruk, V.V., Nefedova, I.N. & Dunaeva, T.N. 1956. On the importance of the small mammals self-defence against the larvae and nymphs of the ixodid ticks. - Zool. Zh. 35: 1717 - 1723. (In Russian).
- Lees, A.D. & Milne, A. 1951. The seasonal and diurnal activities of individual sheep ticks (Ixodes ricinus L.). - Parasitology 41: 189 - 208.
- Macleod, J. 1934. Ixodes ricinus in relation to its physical environment: the influence of climate on development. - Parasitology 26: 282 - 305.
- Macleod, J. 1935. Ixodes ricinus in relation to its physical environment. II. The factors governing survival and activity. - Parasitology 27: 123 - 144.
- Mermod, C., Aeschlimann, A. & Graf, J.-F. 1973. Écologie et éthologie d'Ixodes ricinus Linné 1758, en Suisse (Acarina, Ixodoidea). Première note: Fluctuations numériques. - Acarologia 15: 197 - 205.
- Miller, R.S. 1955. Activity rhythms in the wood mouse, Apodemus sylvaticus, and the bank vole, Clethrionomys glareolus. - Proc. Zool. Soc. Lond. 125: 505 - 519.
- Mohr, C.O. 1961. Relation of ectoparasite load to host size and standard range. - J. Parasitol. 47: 978 - 984.
- Nikitina, N.A. & Aristova, V.A. 1964. Protective reactions against ticks in rodents. - Med. Parazit. Moskva 33: 141 - 144. Transl. 247 Dep. Med. Zool. U.S. Naval Med. Res. Unit No. 3. Cairo, Egypt.
- Nikitina, N.A. & Zhmaeva, Z.M. 1963. Factors determining the rate of infestation of different species of hosts by ticks. - Med. Parazit. Moskva 32: 39 - 43.
- Nikitina, N.A., Karulin, B.E., Litvin, V.Yu., Khlyap, L.A., Albov, S.A., Sushkin, N.D. & Okhotsky, Yu.V. 1977. On the size of daily territory and probable structure of individual ranges in some species of rodents. - Zool. Zh. 56: 1860 - 1868. (In Russian, English summary).

- Randolph, S.E. 1975. Patterns of distribution of the tick Ixodes trianguliceps Birula on its hosts. - J. Anim. Ecol. 44: 451 - 474.
- Rick, R.F. 1962. Studies on the reactions of animals to infestation with ticks. VI. Resistance of cattle to infestation with the tick Boophilus microplus (Canestrini). - Austr. J. agric. Res. 13: 532 - 550.
- Roberts, J.A. 1968. Resistance of cattle to the tick Boophilus microplus (Canestrini). II. Stages of the life cycle of the parasite against which resistance is manifested. - J. Parasit. 54: 667 - 673.
- Trager, W. 1939. Acquired immunity to ticks. - J. Parasit. 25: 57 - 81.

	<u>Sorex</u> <u>araneus</u>	<u>Clethrionomys</u> <u>glareolus</u>	<u>Apodemus</u> <u>sylvaticus</u>
<u>SPRING</u>			
No. of hosts	51	81	98
% infested hosts	86.3	91.4	95.9
I. ricinus/host ($\bar{x}$)	12.6	12.7	28.8
Variance (s^2)	307	193	953
$\frac{s^2}{\bar{x}}$	24.4	15.2	33.1

<u>AUTUMN</u>			
No. of hosts	129	233	276
% infested hosts	36.4	46.4	49.6
I. ricinus/host ($\bar{x}$)	0.7	1.2	1.9
Variance (s^2)	2.3	4.4	14.4
$\frac{s^2}{\bar{x}}$	3.3	3.7	7.6

<u>Student's</u> <u>t-test of $\bar{x}$</u>	<u>SPRING</u>		<u>AUTUMN</u>	
S.a.-C.g.	NS		t=2.62	0.05 > P > 0.01
S.a.-A.s.	t=6.60	P < 0.001	t=4.54	P < 0.001
C.g.-A.s.	t=4.63	P < 0.001	t=37.14	P < 0.001

Tab. 1. Infestation characteristics of Ixodes ricinus larvae on three small mammal host species during periods of high and low tick activity, in May and November 1964 - 1968 at Kullaberg, South Sweden. S.a. = Sorex araneus, C.g. = Clethrionomys glareolus, A.s. = Apodemus sylvaticus.

	<u>C. glareolus</u>		<u>A. sylvaticus</u>	
	♂♂	♀♀	♂♂	♀♀
<u>SPRING</u>				
No. of adult hosts	51	26	52	31
% infested hosts	94.1	84.6	94.2	96.8
I. ricinus/host ($\bar{x}$)	16.9	6.0	26.4	33.9
Variance (s^2)	234	49.0	549	1620
$\frac{s^2}{\bar{x}}$	13.8	8.2	20.8	47.8

<u>AUTUMN</u>				
No. of subadult hosts	111	105	108	118
% infested hosts	48.7	44.8	49.1	55.9
I. ricinus/host ($\bar{x}$)	1.4	0.9	1.9	2.4
Variance (s^2)	5.0	2.2	12.4	20.2
$\frac{s^2}{\bar{x}}$	3.6	2.4	6.5	8.4

<u>Student's</u>		<u>SPRING</u>		<u>AUTUMN</u>	
<u>t-test</u>					
C.g.:	♂♂-♀♀	t=4.29	P < 0.001	t=1.98	0.01 < P < 0.05
A.s.:	♂♂-♀♀	t=0.95	NS	t=0.94	NS

Tab. 2. Infestation characteristics of Ixodes ricinus larvae on different sexes of two host species during periods of high and low tick activity in May and November 1964 - 1968 at Kullaberg, South Sweden. C.g. = Clethrionomys glareolus, A.s. = Apodemus sylvaticus.

	n	Mean number engorged larvae	SE	Range	P	Feeding period (hours)	SE	Range	P
<i>C. glareolus</i>	54	2.43	0.26	0 - 8	$t = 10.79$ $P < 0.001$	71	1.75	38 - 128	NS
<i>A. sylvaticus</i>	27	15.93	1.22	7 - 26		71	2.21	34 - 145	

Tab. 3. Feeding period and mean number of engorged I. ricinus larvae on C. glareolus and A. sylvaticus under laboratory conditions. 30 ticks were placed on each host animal.

	15 minutes	60 minutes
<u>C. glareolus</u>		
Dead	20	50
Alive	19	47
<u>A. sylvaticus</u>		
Dead	1	6
Alive	5	8

Tab. 4. "Infestation success" (%) 15 minutes and 60 minutes after transference of I. ricinus larvae to dead and live specimens of C. glareolus and A. sylvaticus. For dead animals the figures for 15 minutes refer to ticks which had not moved forward. For live animals the figures cover ticks which had left the host.

Fig. 1. Frequency distribution of Ixodes ricinus on hosts during periods of high and low tick activity. ■ observed frequency; □ negative binomial.

spring: A - B. C.glareolus: A. adult ♂♂ , B. adult ♀♀

C - D. A.sylvaticus: C. adult ♂♂ , D. adult ♀♀

autumn: E - F. C.glareolus: E. subadult ♂♂ , F. subadult ♀♀

G - H. A.sylvaticus: G. subadult ♂♂, H. subadult ♀♀

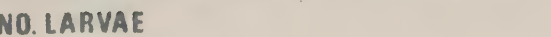
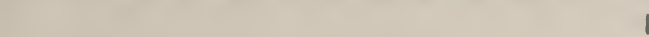
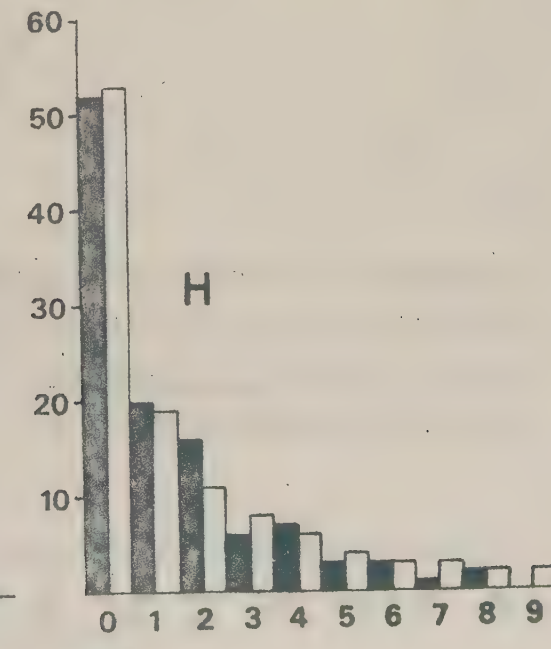
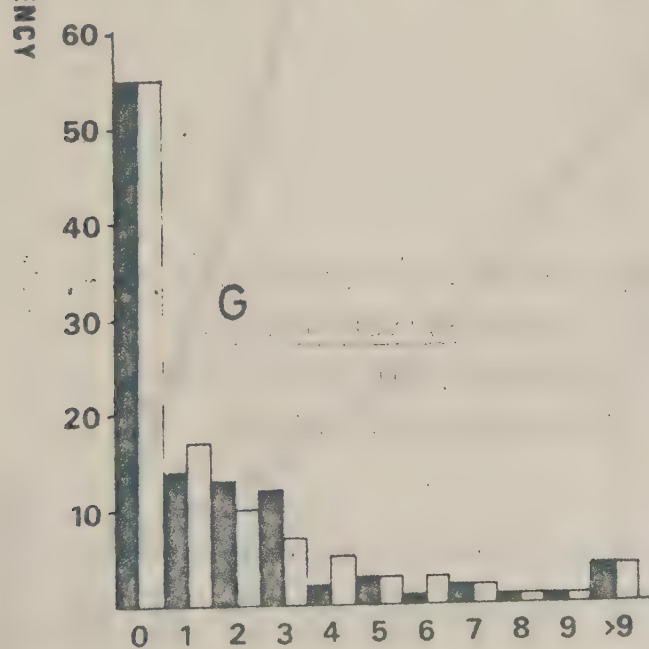
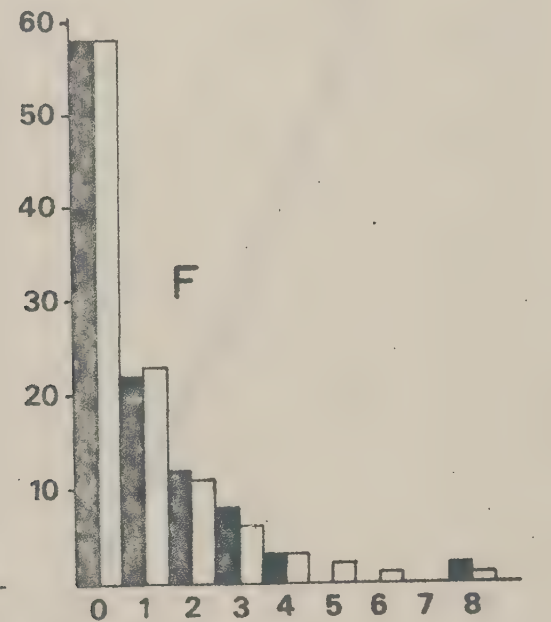
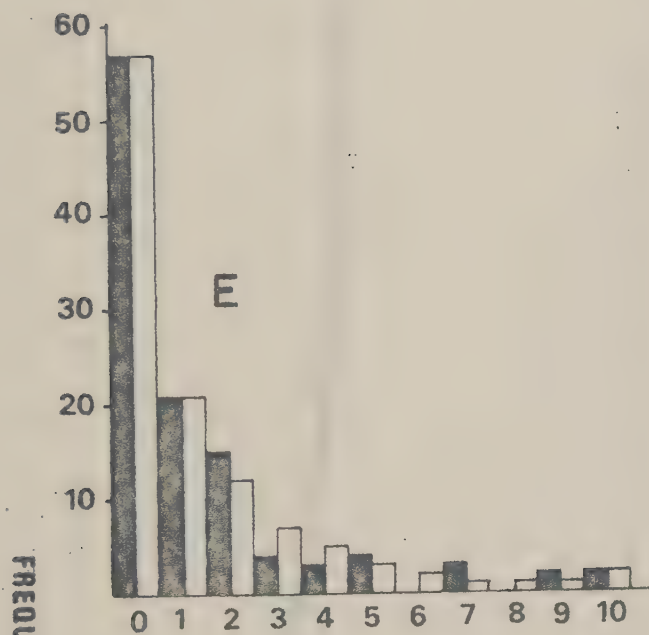
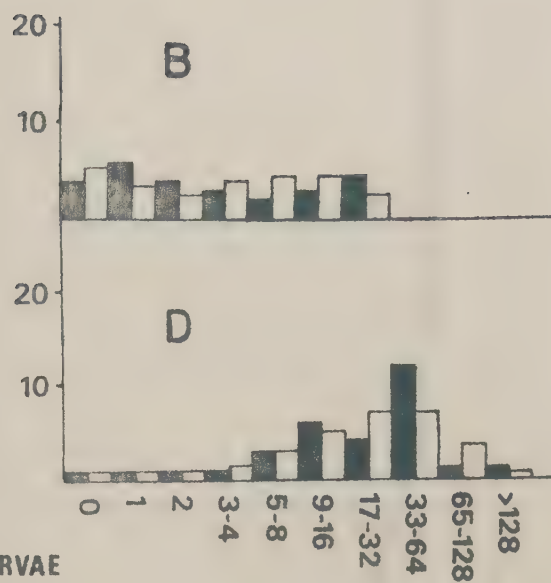
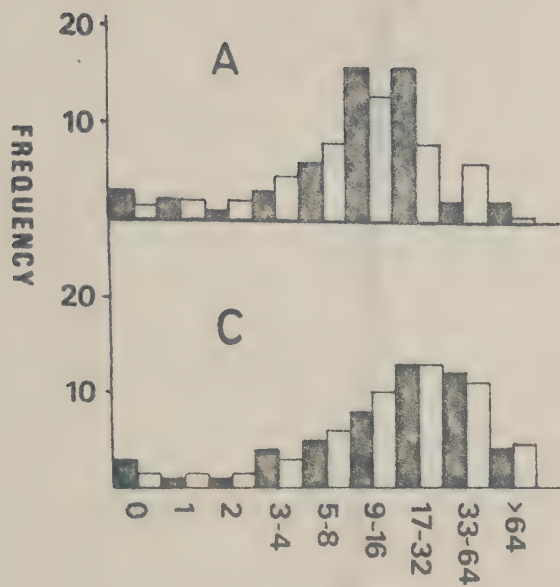
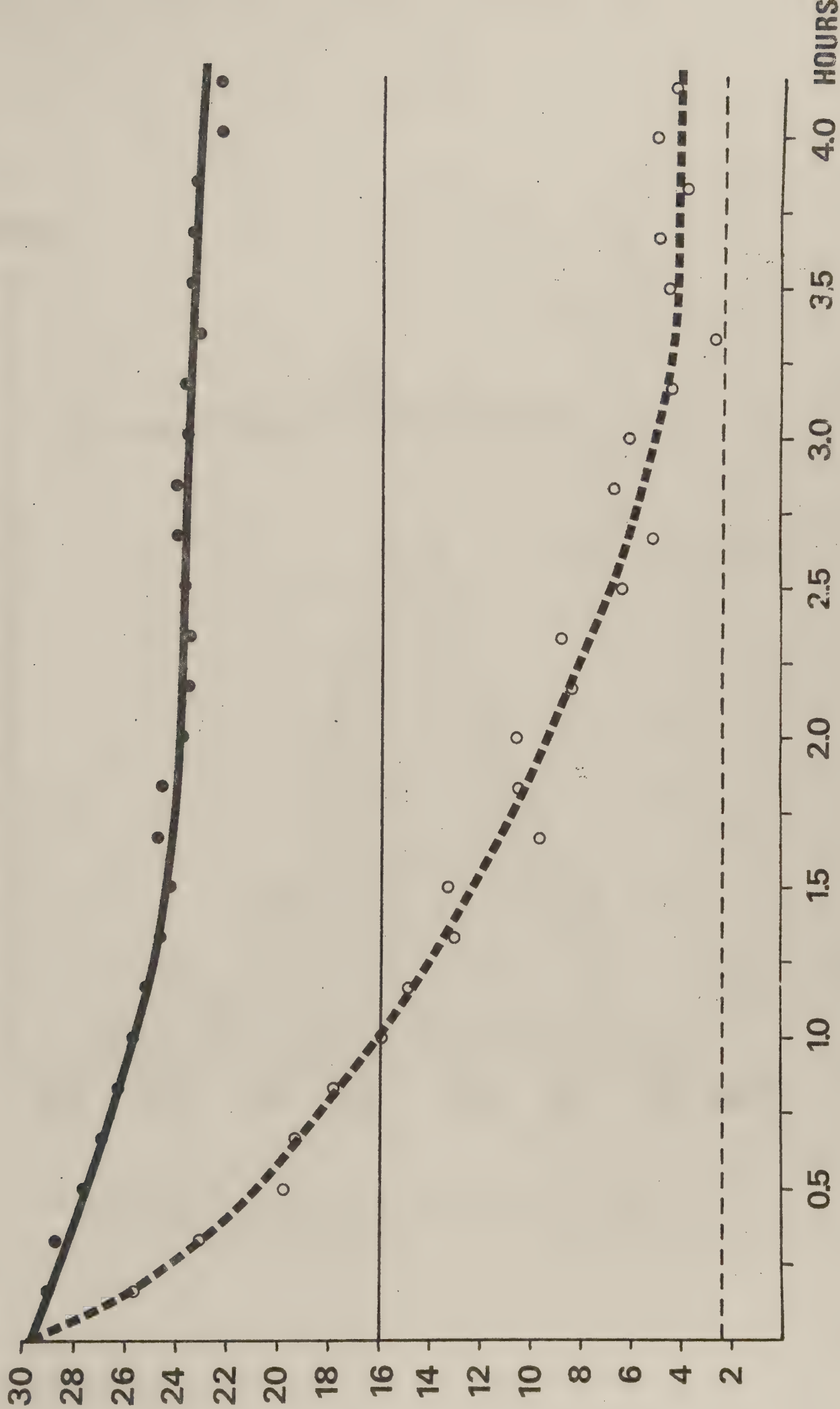
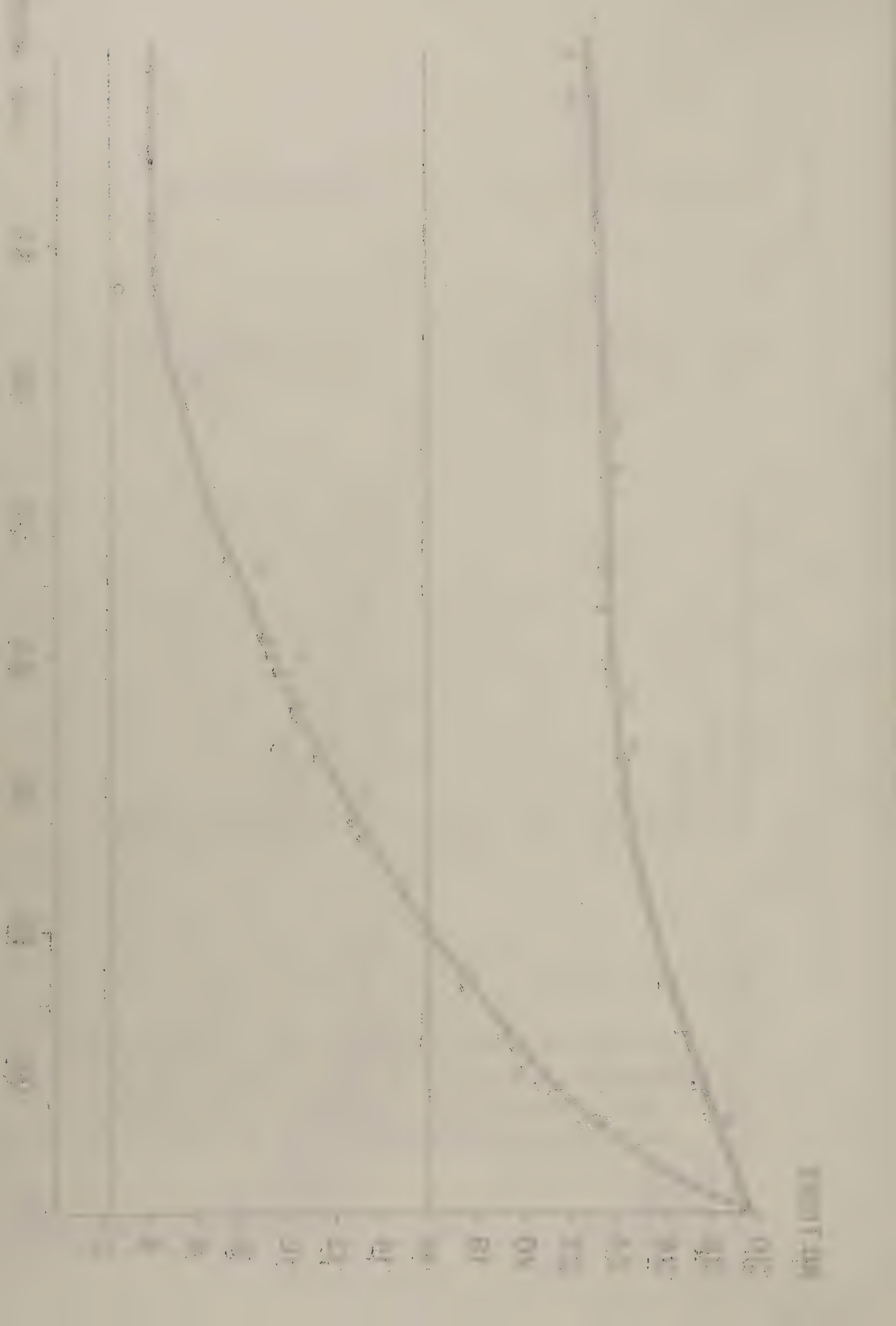


Fig. 2. Emigration of unfed I. ricinus larvae in relation to time after introduction. Solid lines: A. sylvaticus, dotted lines: C. glareolus. The horizontal lines refer to the engorged part of the introduced population.

NO. TICKS





NO. TICKS

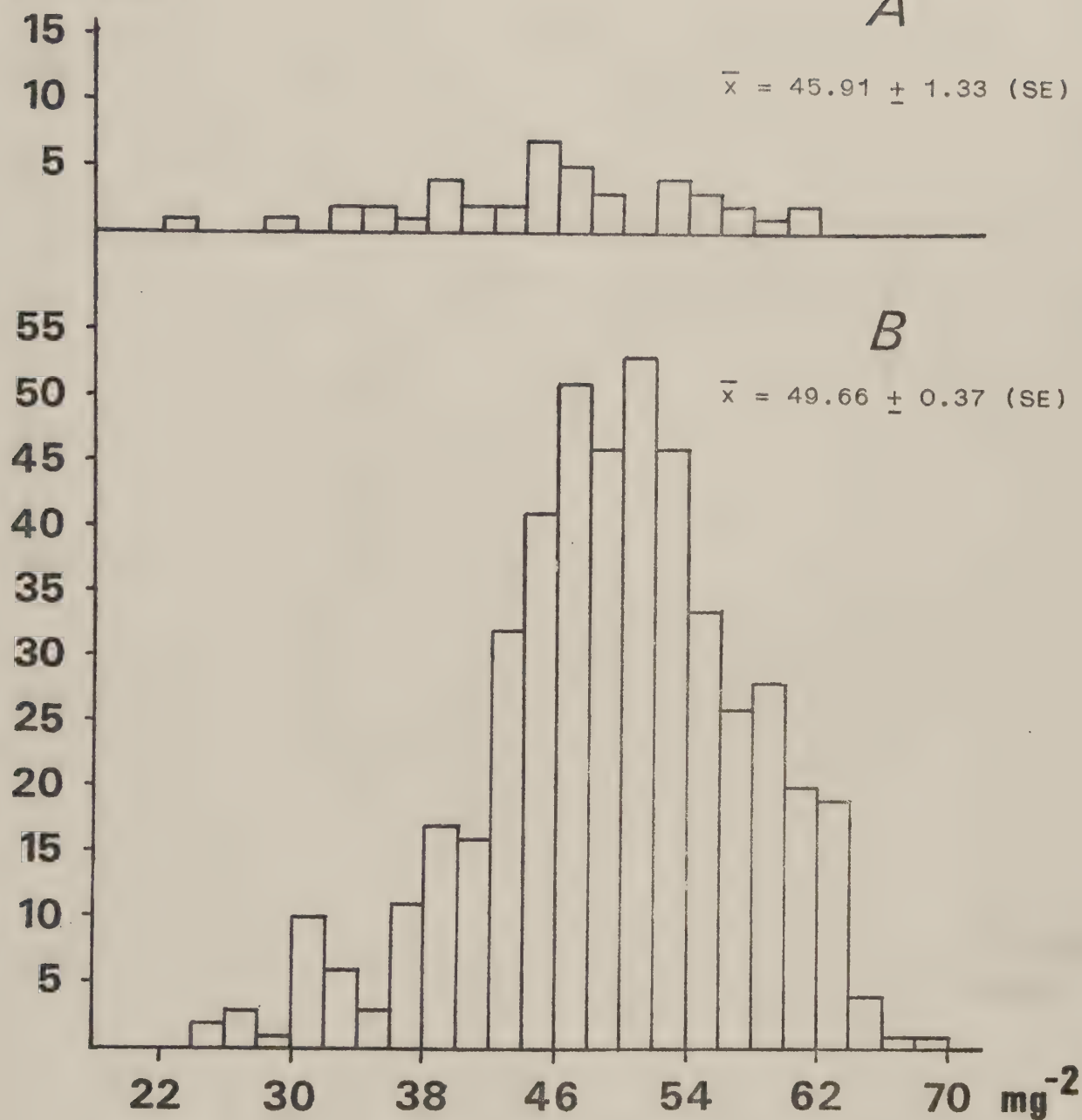


Fig.3. Weight distribution of engorged *I. ricinus* larvae on A. *C. glareolus* and B. *A. sylvaticus*.

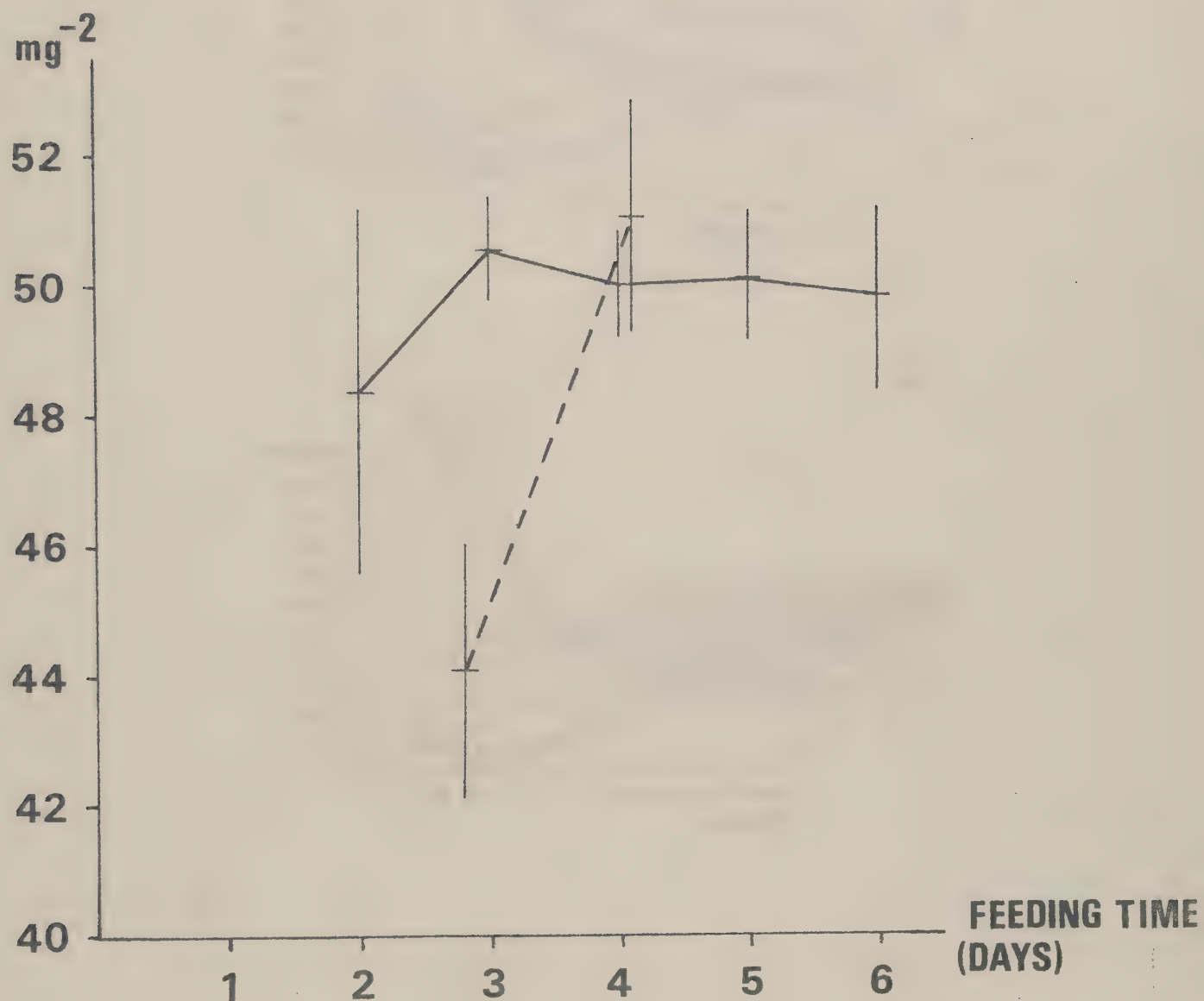


Fig.4. Mean weight, standard error, and feeding period of *Ixodes ricinus* larvae, fed on *A.sylvaticus* and *C.glareolus* under laboratory conditions. The data of feeding period on *C.glareolus* have been pooled. Solid line: *A.sylvaticus*, dotted line: *C.glareolus*.

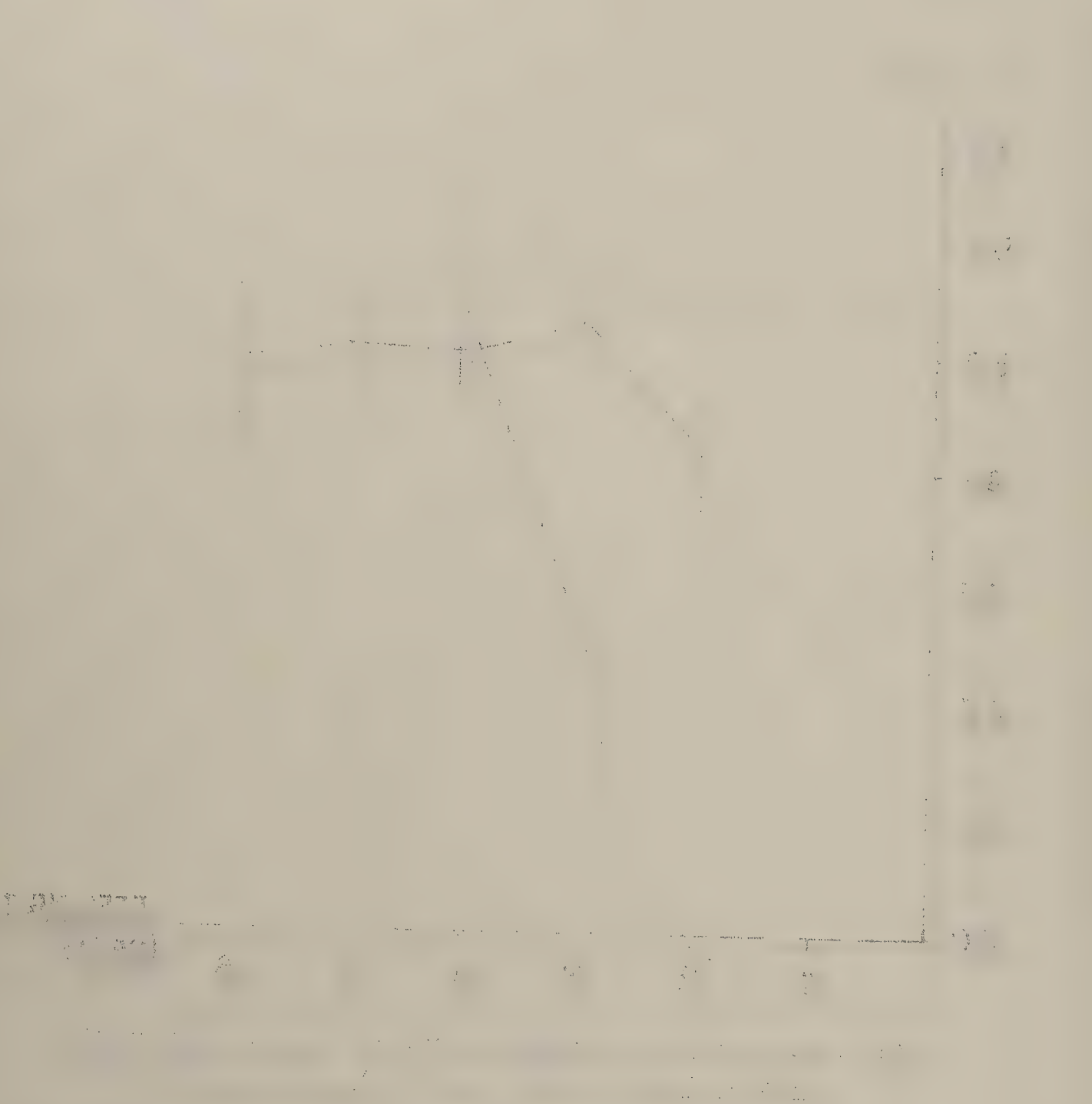
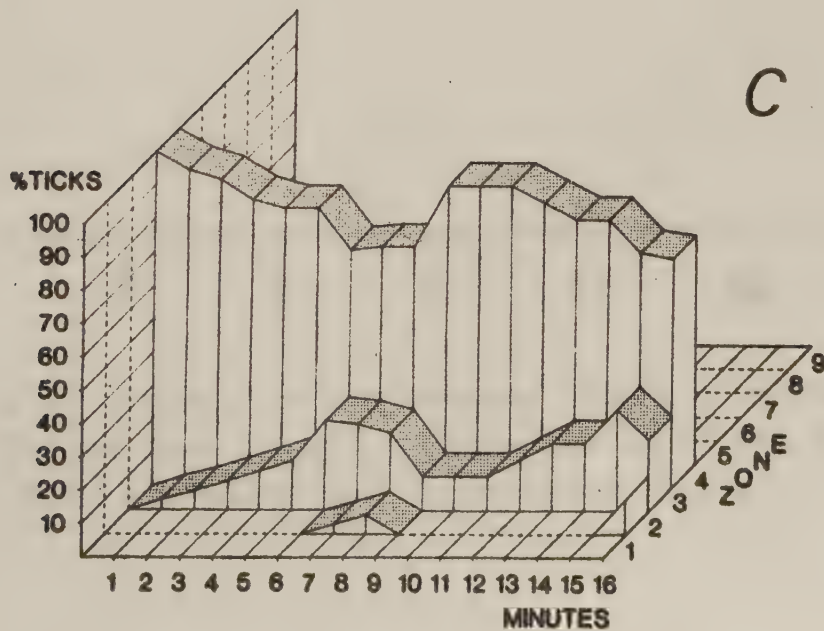
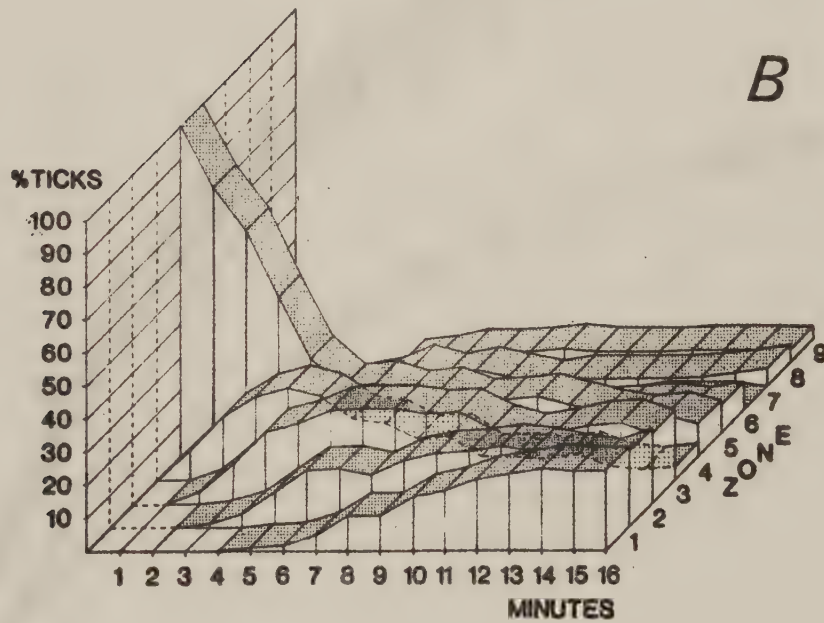
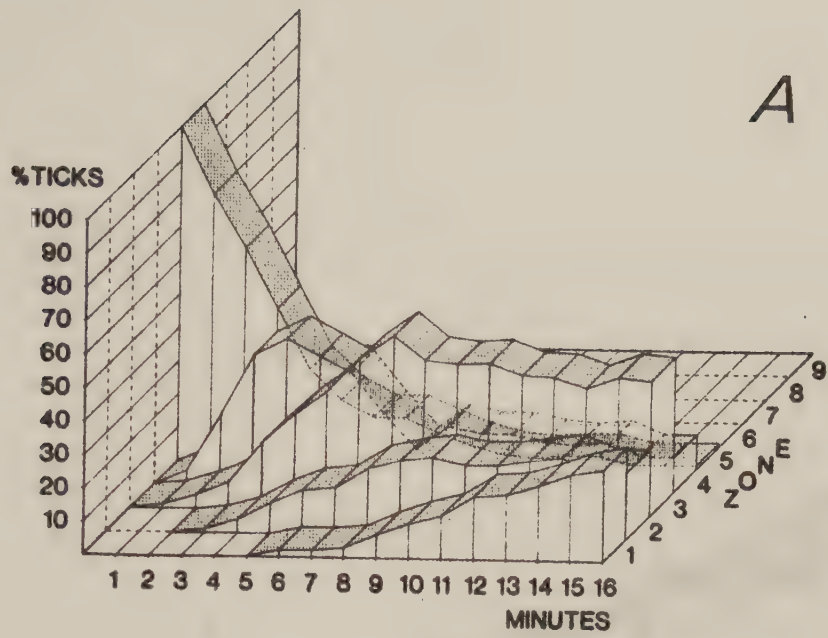
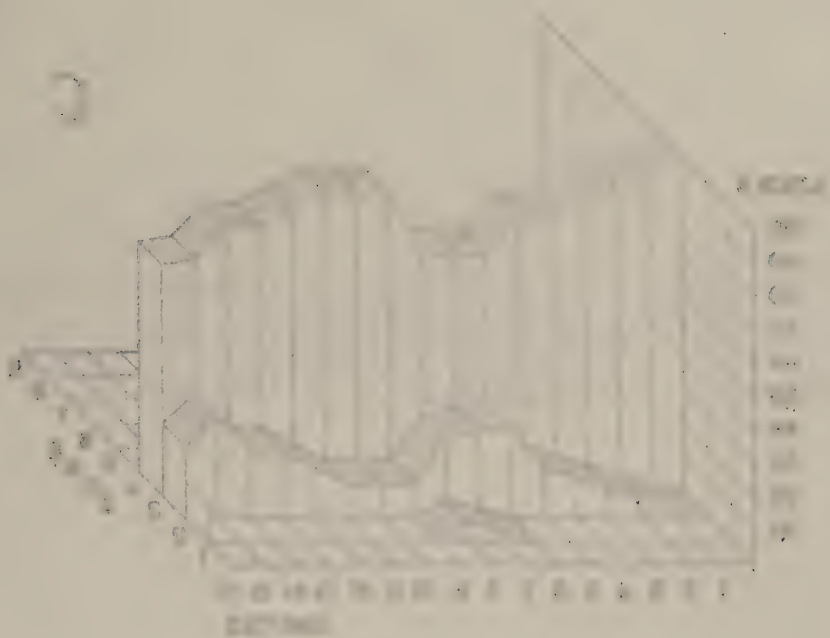


Fig. 5. Spatial frequency distribution of I. ricinus larvae
on host species in relation to time after introduction.
A: A. sylvaticus, B: C. glareolus, C: S. araneus





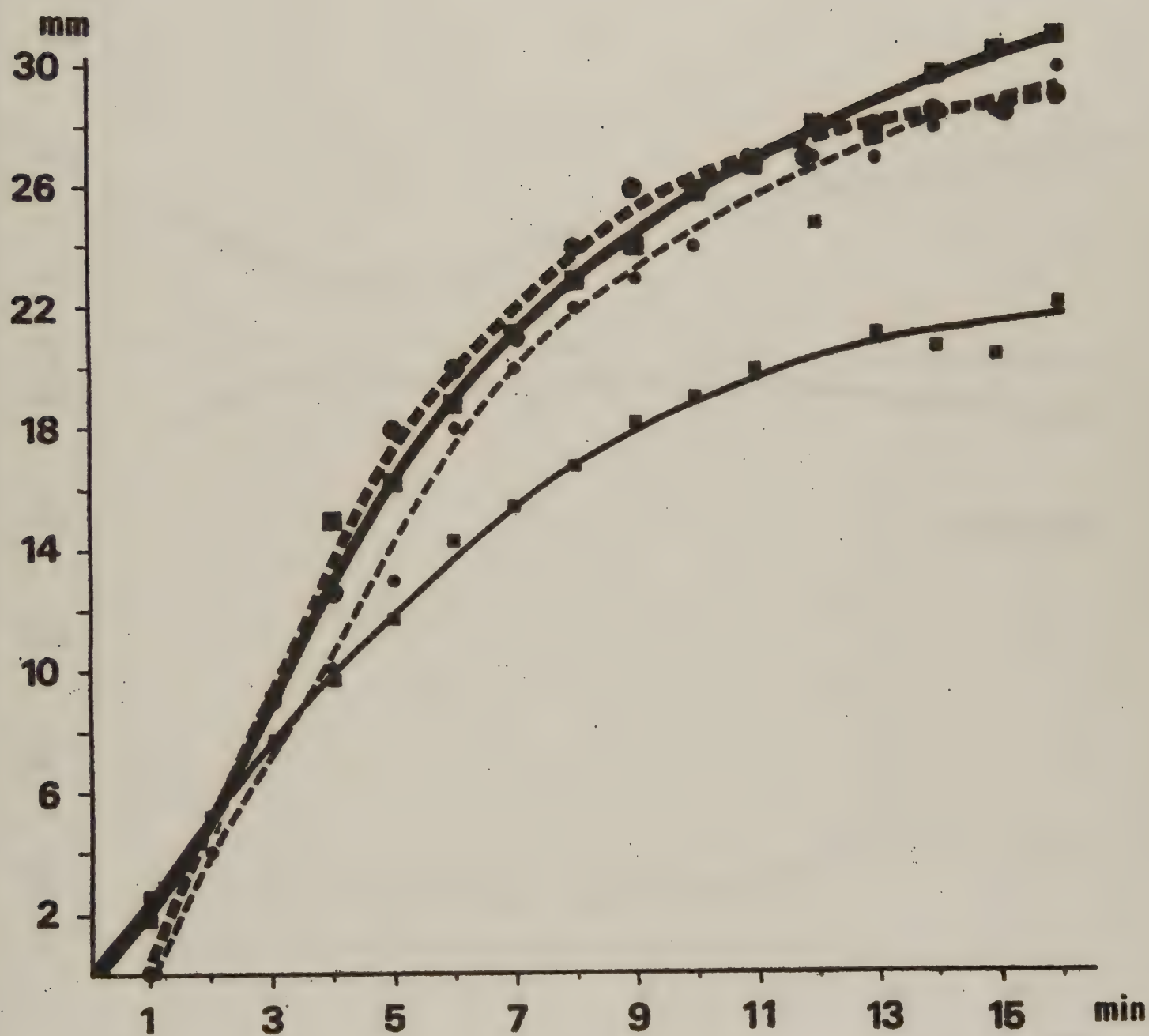


Fig.6. Rate of movement of the average (solid line) and the median (dotted line) *I. ricinus* larvae on the fur of *A. sylvaticus* (bold) and *C. glareolus* (thin).

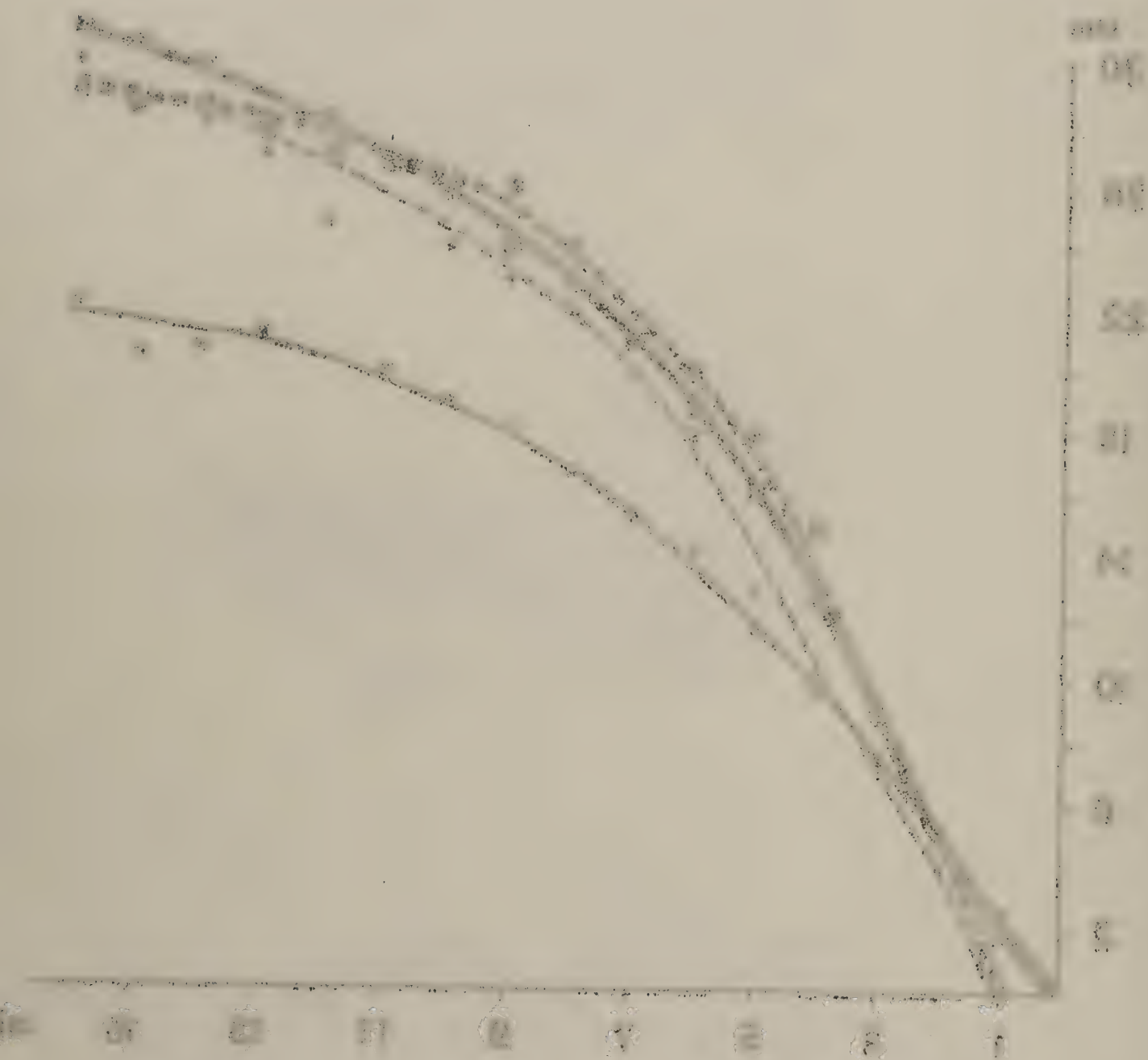


Fig. 6. Rate of movement of the average (solid line) and the median (dotted line) larvae on the top of A. sylvaticus (solid) and C. glaucus (dotted).

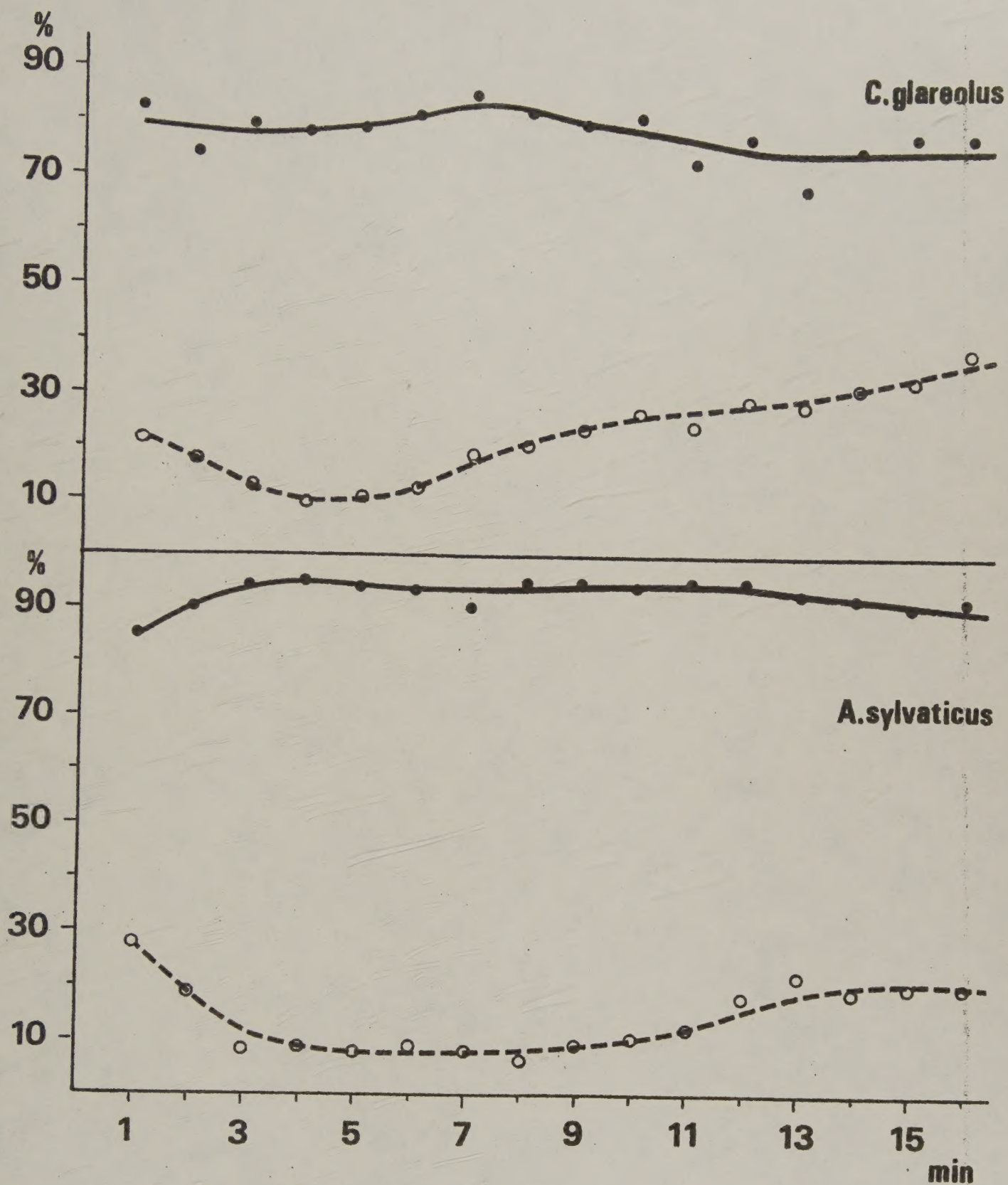


Fig.7. Orientation of *I. ricinus* larvae on *C. glareolus* and *A. sylvaticus* during the first 16 minutes after transference to the host. Directed forward (solid line), hiding in the fur (dotted line).

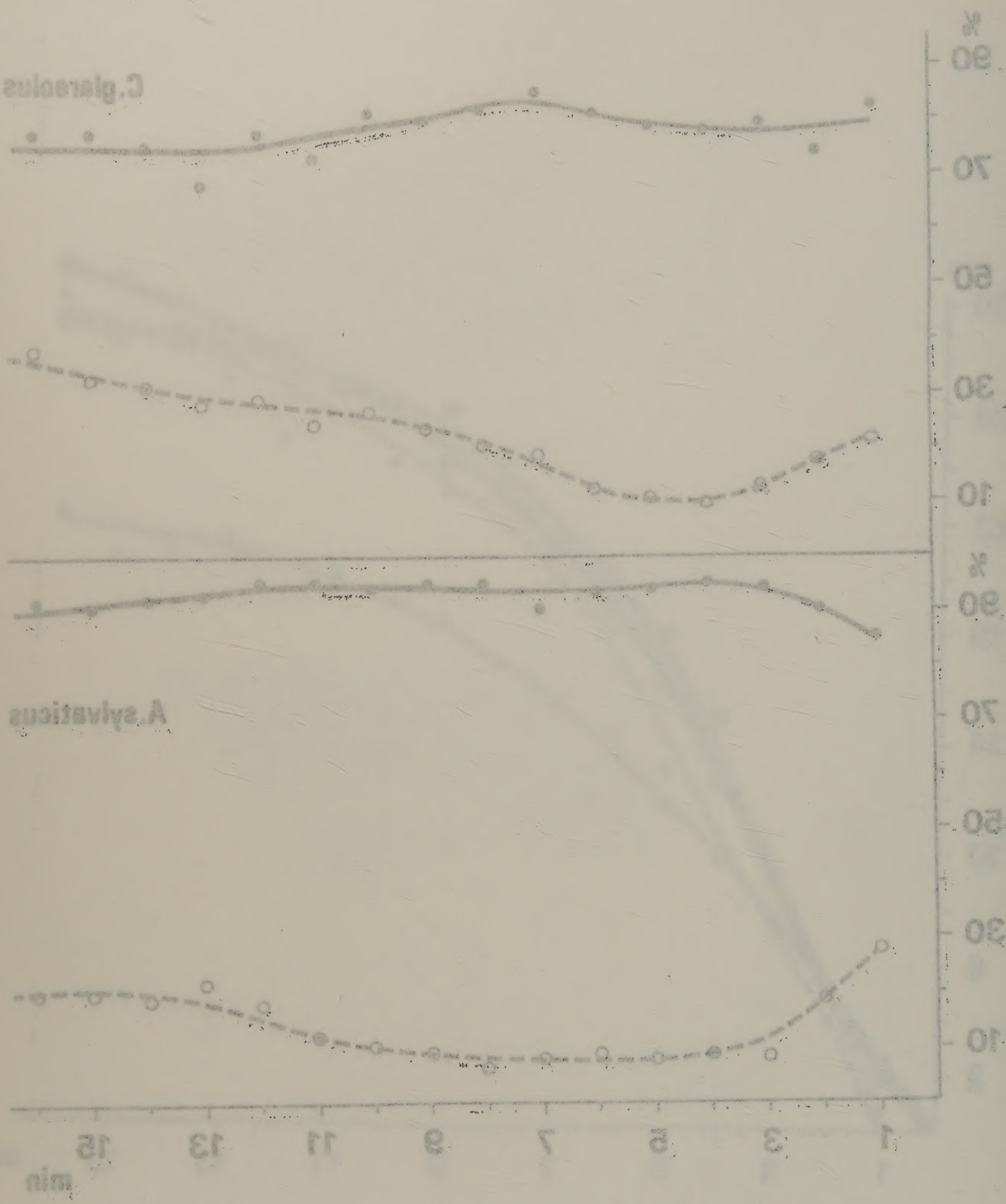


Fig. 7. Orientation of *I. ricinus* larvae on *C. glaucus* and *A. sylvaticus* during the first 15 minutes after transference to the host. Directed forward (solid line), hiding in the fur (dotted line).

